The Temporal Lobes

When he was 40 years old, H. H., a successful corporate lawyer with a wife and two school-age children, was finding his job increasingly stressful. His wife was taken off guard when he suddenly announced that he was quitting his law firm. He complained of being so stressed that he simply could not remember cases on which he was working and felt that he could not continue as a lawyer. He had no plan about how he would support his family but, curiously, he seemed unconcerned about it.

A couple weeks later, H. H. shaved his hair off, donned a flowing robe, and left his family to join a fringe religious group. His wife of 15 years was stunned by this sudden change in behavior: up to this point, H. H. had been an atheist. She was notified a couple of weeks later that he had collapsed with a seizure while handing out flowers and peace pamphlets in a large U.S. airport. He was taken to a hospital in a confused state, and a neurological examination revealed a left-temporal-lobe tumor. Fortunately, it was operable and was removed.

H. H. was aphasic after his surgery, but this condition cleared in a matter of weeks. He was left with enduring word-finding difficulties, problematic only when he was tired. He continued to complain of verbal memory problems, however. And his wife said that his personality remained different from what it had been, largely because he remained religious. Eventually, H. H. successfully returned to his law firm, although with a reduced caseload from that of his pretumor days.

H. H. showed typical symptoms of temporal-lobe disorder, including radical changes in affect and personality, memory disturbance, and at least a transient disturbance of language. In this chapter, we survey the anatomy of the temporal lobe, present a theoretical model of its function, describe the basic symptoms of damage to it, and briefly describe clinical tests of temporal-lobe function.

Anatomy of the Temporal Lobe

The temporal lobe comprises all the tissue that lies below the Sylvian sulcus and anterior to the occipital cortex (Figure 15.1). Subcortical temporal-lobe structures include the limbic cortex, the amygdala, and the hippocampal formation (Figure 15.2). Connections to and from the temporal lobe extend throughout the brain.

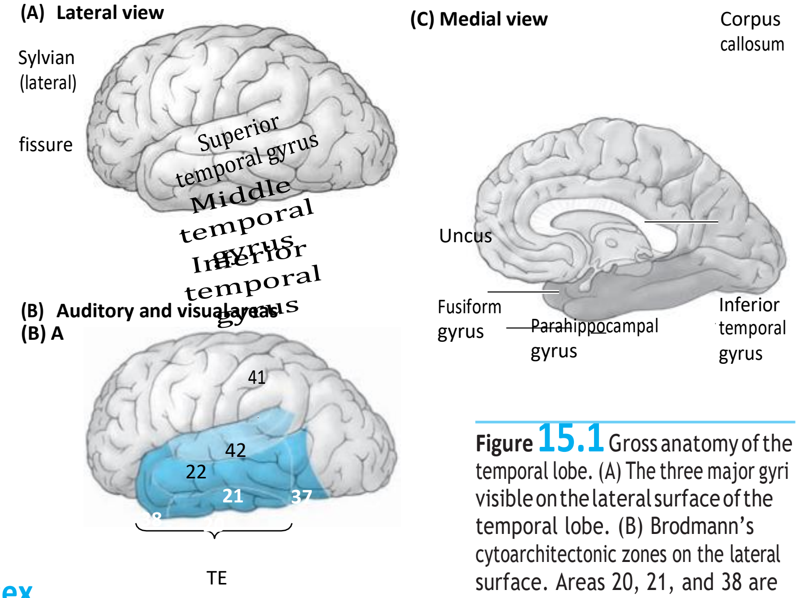


Figure 15.1 Gross anatomy of the temporal lobe. (A) The three major gyri visible on the lateral surface of the temporal lobe. (B) Brodmann's cytoarchitectonic zones on the lateral surface. Areas 20, 21, and 38 are often referred to by von Bonin and Bailey's designation TE. (C) The gyri visible on a medial view of the temporal lobe. The uncus refers to the anterior extension of the hippocampal formation. The parahippocampal gyrus includes areas TF and TH.

Subdivisions of the Temporal Cortex

Brodmann identified 10 temporal areas, but many more areas in the monkey were identified in more-recent studies (see Felleman and van Essen's map, Figure 10.19). Likely there are more areas in the human as well. We can divide the temporal regions on the lateral surface into those that are auditory (Brodmann's areas 41, 42, and 22 in Figure 15.1B) and those that form the ventral visual stream on the lateral temporal lobe (areas 20, 21, 37, and 38 in Figure 15.1B). The visual regions are often referred to as inferotemporal cortex or by von Economo's designation, TE.

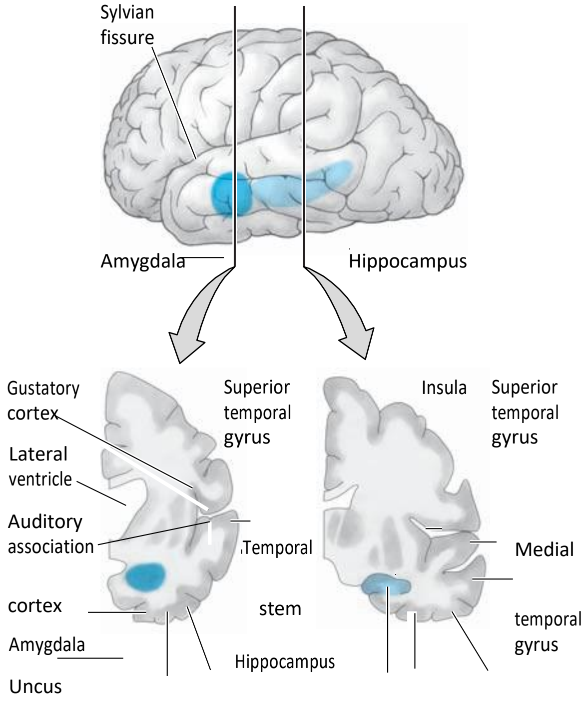


Figure 15.2 Internal structure of the temporal lobe. (Top) Lateral view of the left hemisphere illustrating the relative positions of the amygdala and hippocampus buried deep in the temporal lobe. The vertical lines

Inferior temporal gyrus

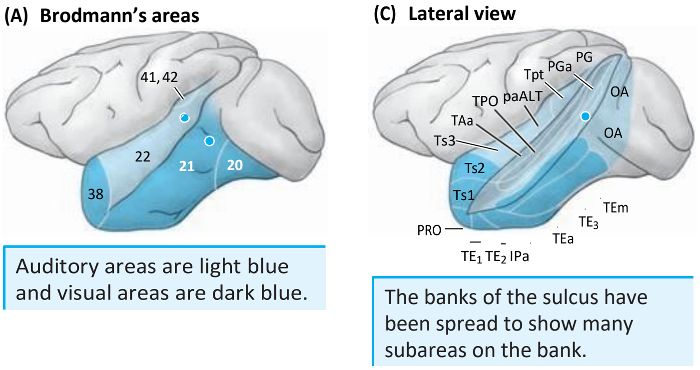
Medial temporal gyrus

Hippocampal gyrus

Fusiform gyrus

Inferior temporal gyrus

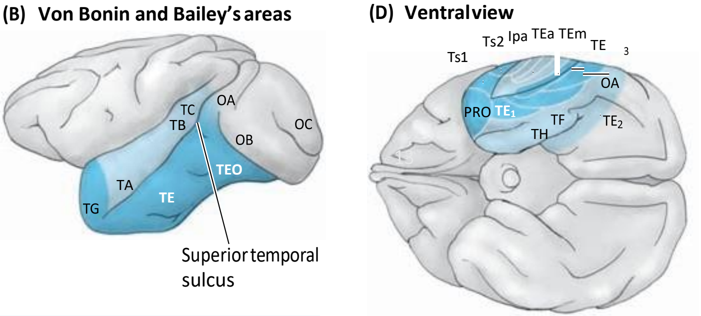
indicate the approximate location of the sections in the bottom illustration. (Bottom) Frontal sections through the left hemisphere illustrating the cortical and subcortical regions of the temporal lobe.


(A) Brodmann's areas

Auditory areas are light blue and visual areas are dark blue.

(C) Lateral view

The banks of the sulcus have been spread to show many subareas on the bank.


(B) Von Bonin and Bailey's areas

(D) Ventral view

Figure 15.3 Cytoarchitectonic regions of the temporal cortex of the rhesus monkey. (A) Brodmann's areas. (B) Von Bonin and Bailey's areas. (C and D) Lateral and ventral views of Seltzer and Pandya's parcellation showing the multimodal areas in the superior temporal sulcus. The sulcus has been opened up to reveal many subareas on its banks. These subareas are normally not visible from the surface.

The sulci of the temporal lobe contain a lot of cortex, as can be seen in Figure 15.2. In particular, the Sylvian fissure contains tissue forming the *insula,* which includes the gustatory cortex as well as the auditory association cortex. The superior temporal sulcus, which separates the superior and middle temporal gyri, also contains a significant amount of neocortex, which can be divided into many subregions (Figure 15.3). The cortex of the superior temporal sulcus is multimodal, receiving input from auditory, visual, and somatic regions, as well as from the other two polymodal regions (frontal and parietal) and the paralimbic cortex.

The medial temporal region (limbic cortex) includes the amygdala and adjacent cortex (uncus), the hippocampus and surrounding cortex (subiculum, entorhinal cortex, perirhinal cortex), and the fusiform gyrus. The entorhinal cortex is Brodmann's area 28, and the perirhinal cortex comprises Brodmann's areas 35 and 36. Cortical areas TH and TF at the posterior end of the temporal lobe are often referred to as the *parahippocampal cortex* (see Figure 15.3). The fusiform gyrus and inferior temporal gyrus are functionally part of the lateral temporal cortex (see Figure 15.2).

Connections of the Temporal Cortex

The temporal lobes are rich in internal connections, afferent projections from the sensory systems, and efferent projections to the parietal and frontal association regions, limbic system, and basal ganglia. The neocortex of the left and right temporal lobes is connected by the corpus callosum, whereas the medial temporal cortex and amygdala are connected by the anterior commissure.

The results of studies on the temporal–cortical connections of the monkey reveal five distinct types of cortical–cortical connections, which are illustrated in Figure 15.4:

1. *A hierarchical sensory pathway.* The hierarchical progression of connections emanate from the primary and secondary auditory and visual areas, ending in the temporal pole. The visual projections form the ventral stream of visual processing, whereas the auditory projections form a parallel ventral stream of auditory processing (see Figure 15.4A).
2. *A dorsal auditory pathway.* Traveling from the auditory areas to the posterior parietal cortex, this pathway is analogous to the dorsal visual pathway and thus concerned with directing movements with respect to auditory information (see Figure 15.4A).

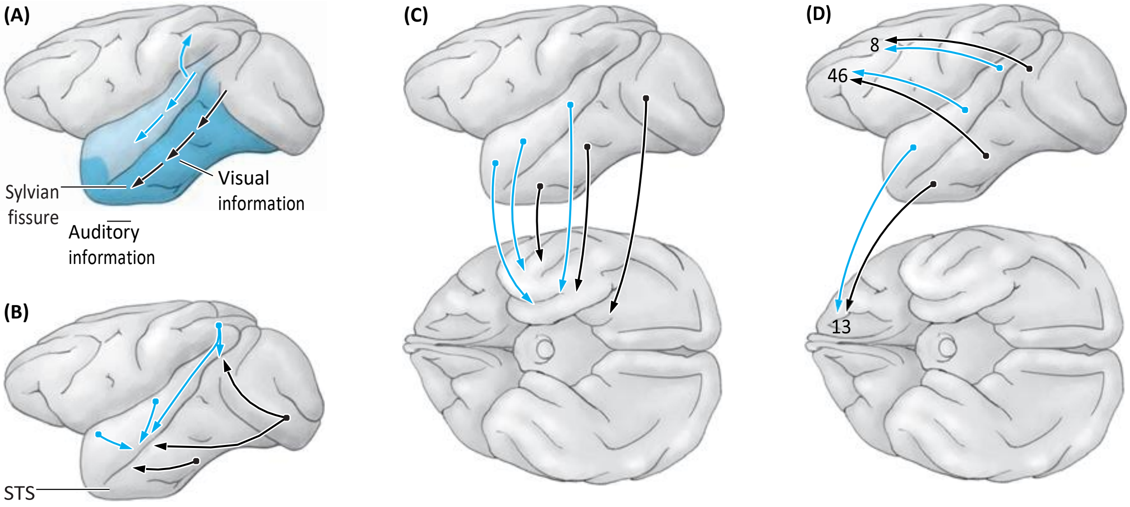


Figure 15.4 Major intracortical connections of the temporal lobe. (A) Auditory and visual information progress ventrally from the primary regions toward the temporal pole, en route to the medial temporal regions. Auditory information also forms a dorsal pathway to the posterior parietal cortex. (B) Auditory, visual, and somatic outputs go to the multimodal regions of the superior temporal sulcus. (C) Auditory and visual information goes to the medial temporal region, including the amygdala and the hippocampal formation. (D) Auditory and visual information goes to two prefrontal regions, one on the dorsolateral surface and the other in the orbital region (area 13).

3. *A polymodal pathway.* This pathway is a series of parallel projections from the visual and auditory association areas into the polymodal regions of the superior temporal sulcus (see Figure 15.4B).
4. *A medial temporal projection.* The projection from the auditory and visual association areas into the medial temporal, or limbic, regions goes first to the perirhinal cortex, then to the entorhinal cortex, and finally into the hippocampal formation or the amygdala or both (see Figure 15.4C). The hippocampal projection is a major one, forming the **perforant pathway.** A disturbance of this projection results in a major dysfunction in hippocampal activity.
5. *A frontal-lobe projection.* This series of parallel projections reaches from the association areas to the frontal lobe (see Figure 15.4D).

These five projection pathways presumably subserve different functions, which will become apparent in the next section. Briefly, the hierarchical sensory pathway probably subserves stimulus recognition; the dorsal auditory pathway may play some role in detecting the spatial location of auditory inputs; the polymodal pathway probably underlies stimulus categorization; the medial temporal projection is crucial to long-term memory; and the frontal-lobe projection is necessary for various aspects of movement control, short-term memory, and affect.

A Theory of Temporal-Lobe Function

The temporal lobe does not have a unitary function, in that it houses the primary auditory cortex, the secondary auditory and visual cortex, the limbic cortex, and the amygdala and hippocampus. On the basis of the cortical anatomy, we can identify three basic sensory functions of the temporal cortex: one concerned primarily with the processing of auditory input, another specialized for visual object recognition, and still another associated with long-term storage of sensory input (that is, memory). The hippocampus works in concert with the object-recognition and memory functions of the neocortex and plays a special role in organizing the memory of objects in space. The remaining temporal-lobe region, the amygdala, adds affective tone (that is, emotion) to sensory input and memories.

Temporal-lobe functions are best understood by considering how the brain analyzes sensory stimuli as they enter the nervous system. Imagine that you are hiking in the woods. On your journey, you notice many different birds, and you decide to keep a mental list of the species that you encounter so that you can tell your sister, who is an avid birder. As you walk along, you suddenly stop and back up—you have encountered a rattlesnake in the middle of the path. You decide to change routes and look for birds elsewhere! What temporal-lobe functions took part in your experience?

Sensory Processes

As you searched for different birds, you needed to be aware of specific colors, shapes, and sizes of birds that you might encounter. This process is object recognition and is the function of the ventral visual pathway in the temporal lobe.

You also needed to be able to categorize the birds quickly, because they were often flying away, and you had to do so by using information that varied in perspective from sighting to sighting (for example, lateral view versus rear view). This process of categorization is crucial to both perception and memory and probably depends on the cortex in the superior temporal sulcus. Categorization may require a form of directed attention because certain characteristics of stimuli are likely to play a more important role in classification than others. For example, classifying two different yellow birds requires that attention be directed away from color and focused on shape, size, and other characteristics. Thus, damage to the temporal cortex leads to deficits in identifying and categorizing stimuli. There is no difficulty in locating the stimulus or in recognizing that a stimulus is present, however, because these activities are functions of the posterior parietal and primary sensory areas, respectively.

As you walked along, you also may have heard birdsong, and you needed to match songs with the visual input. This process of matching visual and auditory information is called **cross-modal matching.** It, too, is likely to depend on the cortex of the superior temporal sulcus. As you saw more and more birds, you had to form memories that you could later access. Furthermore, as you saw different birds, you needed to access their names from your memory. These processes of long-term memory depend on the entire ventral visual stream as well as the paralimbic cortex of the medial temporal region.

Affective Responses

When you encountered the snake, you first heard the rattle, which alerted you, and you stopped. As you scanned the ground, you saw and identified the snake, and your heart rate and blood pressure rose. The affective response that you exhibited is a function of the amygdala. The association of sensory input and emotion is crucial for learning because stimuli become associated with their positive, negative, or neutral consequences, and behavior is modified accordingly.

In the absence of this system, all stimuli would be treated as equivalent. Consider the consequences of failing to associate the rattlesnake, which is poisonous, with the consequences of being bitten. Or consider being unable to associate good feelings (such as love) with a specific person. Laboratory animals with amygdala lesions become very placid and do not react emotionally to threatening stimuli. For example, monkeys that were previously terrified of snakes become indifferent to them.

Spatial Navigation

When you changed routes and went elsewhere, you used the hippocampus. The hippocampus contains cells that code places in space; together, these cells allow us to navigate space and to remember where we are.

As we consider these general functions of the temporal lobes, you can see that their loss would have devastating consequences for behavior. There would be an inability to perceive or to remember events, including language. There would be a loss of affect. Note, however, that a person would be able to use the dorsal visual system to make visually guided movements and, under many cir- cumstances, would appear rather normal.

The Superior Temporal Sulcus and Biological Motion

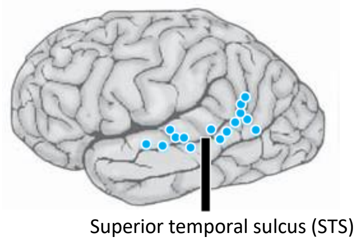
An additional temporal-lobe function was not included in our hiking example. Animals engage in what we can call *biological motion,* or movements that have particular relevance to a species. For example, our eyes, faces, mouths, hands, and bodies make movements that can have social meanings. We shall see that the superior temporal sulcus analyzes these types of movements.

As already mentioned, the superior temporal sulcus receives multimodal inputs, and these inputs play a role in categorizing stimuli. A major category of stimuli is social perception, which includes the analysis of actual or implied bodily movements that provide socially relevant information. This information plays an important role in allowing us to develop hypotheses about the inten- tions of other people, an ability that is sometimes referred to as *theory of mind* or *social cognition.* For example, the direction in which a person's eyes are look- ing provides us with considerable information about what that person is at- tending (or not attending) to.

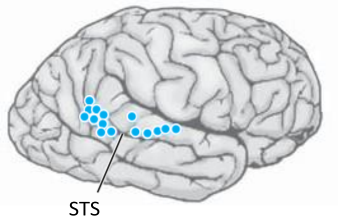
In a nice review, Allison and colleagues propose that cells in the superior temporal sulcus play a key role in social cognition. For example, cells in the monkey superior temporal sulcus respond to various forms of biological motion including the direction of eye gaze, head movement, mouth movement, facial expression, and hand movement. For social animals such as primates, knowledge about biological motion is critical information needed to guess the intentions of others. As illustrated in Figure 15.5, imaging studies show activation along the superior temporal sulcus during the perception of various forms of biological motion.

Figure 15.5 A summary of the activation (shaded areas) of the superior temporal sulcus (STS) region in the left (A) and right (B) hemispheres during the perception of biological motion. (After Allison, Puce, and McCarthy, 2000.)

(A) Left hemisphere



(B) Right hemisphere



An important correlate of mouth movements is vocalization, and so we might predict that regions of the superior temporal sulcus are also implicated in the perception of species-typical sounds. In monkeys, cells in the superior temporal gyrus, which is adjacent to the superior temporal sulcus and sends connections to it, show a preference for "monkey calls," and imaging studies in humans have shown that the superior temporal gyrus is activated both by human vocalizations and by melodic sequences.

We could predict activation in the some part of the superior temporal sulcus in response to the combination of the visual stimulus (mouth movements) and talking or singing. Presumably talking and singing can be perceived as complex forms of biological motion. We could predict that, if people have temporal-lobe injuries that lead to impairments in analyzing biological motion, there is likely to be a correlated deficit in social awareness. Indeed, there is.

Asymmetry of Temporal-Lobe Function

The temporal lobes are sensitive to epileptiform abnormalities, and surgical removal of the abnormal temporal lobe is often of benefit in treating epilepsy. These circumstances also allow neuropsychologists to study the complementary specialization of the temporal lobes.

A comparison of the effects of left and right temporal lobectomy by Brenda Milner and her colleagues revealed that specific memory defects vary according to which side the lesion is on. Damage to the left temporal lobe is associated with deficits in verbal memory; damage to the right with deficits in nonverbal memory (for example, of faces). Similarly, left tempo- ral lesions are associated with deficits in processing speech sounds, whereas right temporal lesions are associated with deficits in processing certain as- pects of music.

Little is known, however, about the relative roles of the left and right temporal lobes in social and affective behavior. Right, but not left, temporal-lobe lesions lead to impairments in the recognition of faces and facial expression; so it seems likely that the two sides play different roles in social cognition. In fact, clinical experience dictates that left and right temporal-lobe lesions have different effects on personality.

Although the left and right temporal lobes are relatively specialized in their functions, do not be overly impressed by the apparent functional asymmetry. Substantial functional overlap is revealed in the relatively minor effects of *unilateral* temporal lobectomy, a striking result considering that such a large zone of the cerebral hemispheres is removed. Recall, for example, the striking recovery of function in H. H., whom we met at the beginning of the chapter. It is incorrect to assume, however, that removing both temporal lobes merely doubles the symptoms of damage seen in unilateral temporal lobectomy. Bilateral temporal-lobe removal produces dramatic effects on both memory and affect that are orders of magnitude greater than those observed subsequent to unilateral lesions.

Symptoms of Temporal-Lobe Lesions

Nine principal symptoms are associated with disease of the temporal lobes: (1) disturbance of auditory sensation and perception, (2) disorders of music perception, (3) disorders of visual perception, (4) disturbance in the selection of visual and auditory input, (5) impaired organization and categorization of sensory

Table 15.1 **Summary of major symptoms of temporal-lobe damage**

Symptoms	Most probable lesion site	Basic reference
Disturbance of auditory sensation	Areas 41, 42, 22	Vignolo, 1969 Hécaen and Albert, 1978
Disturbance of selection of visual and auditory input	Areas TE, superior temporal sulcus	Sparks et al., 1970 Dorff et al., 1965
Disorders of visual perception	Areas TE, superior temporal sulcus, amygdala	Milner, 1968 Meier and French, 1968
Disorders of auditory perception	Areas 41, 42, 22	Samson and Zatorre, 1988 Swisher and Hirsch, 1972
Disorders of music perception	Superior temporal gyrus	Zatorre et al., 2002
Impaired organization and categorization of material	Areas TE, superior temporal sulcus	Wilkins and Moscovitch, 1978 Read, 1981
Poor contextual use	Area TE	Milner, 1958
Disturbance of language comprehension	Area 22 left	Hécaen and Albert, 1978
Poor long-term memory	Areas TE, TF, TH, 28	Milner, 1970
Changes in personality and affect	Areas TE, plus amygdala	Blumer and Benson, 1975 Pincus and Tucker, 1974
Changes in sexual activity	Amygdala, plus?	Blumer and Walker, 1975

input, (6), inability to use contextual information, (7) impaired long-term memory, (8) altered personality and affective behavior, and (9) altered sexual behavior. Table 15.1 summarizes the major symptoms of temporal-lobe damage, lists the most probable lesion sites, and cites basic references. The sections that follow sample the range of temporal-lobe disorders and their clinical assessment.

Disorders of Auditory Perception

Damage to the primary visual or somatic cortex leads to a loss of conscious sensation; so it is reasonable to predict that bilateral damage to the auditory cortex will produce *cortical deafness,* an absence of neural activity in the auditory regions. The results of neither clinical nor animal laboratory studies support this prediction, however. As the Snapshot on page 378 illustrates, auditory hallucinations, which result from spontaneous activity in the auditory regions, are essentially the opposite of cortical deafness. Auditory hallucination is the perception of sounds (hearing voices) that are not actually present. The auditory cortex does play an actual role in discriminating two forms of auditory processing—namely, rapidly presented stimuli and complex patterns of stimuli. Language is fast and must be analyzed quickly, whereas music generally contains relatively slower changes in frequency, but the ear must be sensitive to the small differences in frequency important in music.

Speech Perception

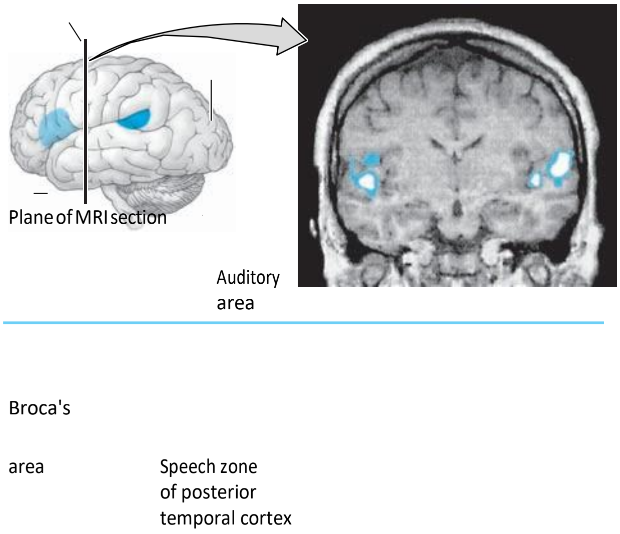
Impaired auditory processing can be seen in the difficulty that temporal-lobe patients have in discriminating speech sounds. Although related to the common complaint among patients with left-temporal-lobe damage that people

SNAPSHOT

Imaging Auditory Hallucinations

Auditory hallucinations are the most common symptom of schizophrenia, being reported by about 65% of people diagnosed with the disease. Auditory hallucinations are not simply sounds; a patient hears fully formed verbal passages that appear to be coming from an external source. The patient's thoughts are usually hostile or paranoid, as in the following example:

> Days later while in the Metropolis again, I was once more startled by those same pursuers, who had threatened me several days before. It was night-time. As before, I could catch part of their talk, but, in the theatre crowds, I could see them nowhere. I heard one them a woman, say: "You can't get away from us; we'll lay for you and get you after a while!" To add to the mystery, one of these "pursuers" repeated my thoughts aloud verbatim. I tried to elude those pursuers as before, but this time I tried to escape from them by means of subway trains, darting up and down subway exits and entrances, jumping on and off trains, until after midnight. But, at every station where I got off a train, I heard the voices of these pursuers as close as ever (L. Percy King, from a letter written in the 1940s protesting the writer's imprisonment in a mental hospital and published in Firth, 1999, p. 414)



fMRI activation of auditory cortex during hallucinations in a schizophrenic subject. (After T. Dierks et al., 1999.)

Dierks and colleagues described an experiment with paranoid schizophrenia patients whose hallucinations could be monitored within one fMRI session. In this study, the verbal hallucinations activated the primary auditory cortex, Broca's area, and the speech zone in the posterior temporal cortex in the left hemisphere. In addition, there was some activation of the limbic areas (see the illustration above).

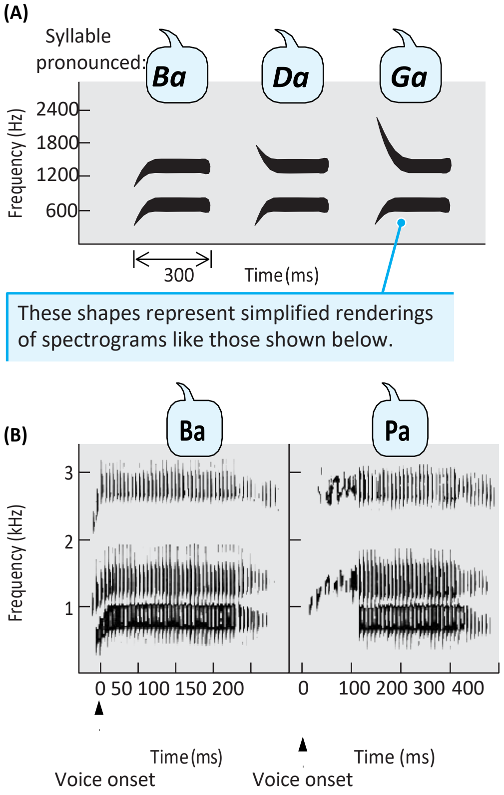
These results suggest that the hallucinations have their origin in the patients' own inner language systems. The researchers propose that activation in the auditory cortex leads to the perception that the voices are coming from an external source. The limbic activity presumably results from the anxiety generated by hearing voices, especially hostile voices.

(T. Dierks, D. E. J. Kinden, M. Jandl, E. Formisano, R. Goebel, H. Lanfermann, and W. Singer. Activation of Heschl's gyrus during auditory hallucinations. *Neuron* 22:615–621, 1999.)

are talking too quickly, the problem is not so much the quickness of the speech but rather the patient's inability to discriminate sounds presented quickly. This difficulty is commonly encountered by normal people trying to learn a new language.

The problem is not just in discriminating the speech sounds, however, but also in judging the temporal order in sounds heard. If a normal subject is presented with two sounds, a temporal separation of only 50 to 60 ms is sufficient to identify which sound was presented first. Subjects with temporal-lobe lesions may require as much as 500 ms between two sounds (a 10-fold increase) to perform at the same level. Each of these audioperceptual impairments appears more severe after left-temporal-lobe lesions than after right-temporal-lobe lesions—a result suggesting that these auditory skills are especially important in the discrimination of speech sounds.

Speech differs from other auditory input in three fundamental ways:



These shapes represent simplified renderings of spectrograms like those shown below.

Figure 15.6 Speech sounds. (A) Schematic spectrograms of three different syllables, each made up of two formants. (B) Spectrograms of syllables differing in voice onset time. (After Springer, 1979.)

1. Speech sounds come largely from three restricted ranges of frequencies, which are known as *formants.* Figure 15.6A illustrates sound spectrograms of different two-formant syllables. The dark bars indicate the frequency bands seen in more detail in Figure 15.6B, which shows that the syllables differ both in the onset frequency of the second (higher) formant and in the onset time of the consonant. Notice that vowel sounds are in a constant frequency band, but consonants show rapid changes in frequency.
2. The same speech sounds vary from one context in which they are heard to another, yet they are all perceived as being the same. Thus, the sound spectrogram of the letter "d" in English is different in the words "deep," "deck," and "duke," yet a listener perceives all of them as "d." The auditory system must have a mechanism for categorizing varying sounds as equivalent, and this mechanism must be affected by experience, because a major obstacle to learning foreign languages in adulthood is the difficulty of learning equivalent sound categories. Thus, a word's spectrogram depends on context—the words that precede and follow it. (There may be a parallel mechanism for musical categorization as well.)
3. Speech sounds change very rapidly in relation to one another, and the sequential order of the sounds is critical to understanding. According to Liberman, we can perceive speech at rates of up to 30 segments per second, although normal speech is on the order of 8 to 10 segments per second. Speech perception at the higher rates is truly amazing, because it far exceeds the auditory system's ability to transmit all the speech as separate pieces of auditory information. For example, nonspeech noise is perceived as a buzz at a rate of only about 5 segments per second. Clearly, language sounds must be recognized and analyzed in a special way by the brain, much as the echolocation system of the bat is specialized in the bat brain. It is likely that the special mechanism for speech perception is in the left temporal lobe. This function may not be unique to humans, because the results of studies in both monkeys and rats have shown specific deficits in the perception of species-typical vocalizations after temporal lesions.

The fact that left-temporal-lobe lesions alter the perception of speech sounds ought not to be surprising: since the time of Wernicke, lesions of the left temporal association cortex (primarily area 22) have been known to produce aphasia (see Chapter 1). The classical view of Wernicke's aphasia is that it is associated with disturbed recognition of words, the extreme form being "word deafness"—an inability to recognize words as such despite intact hearing of pure tones.

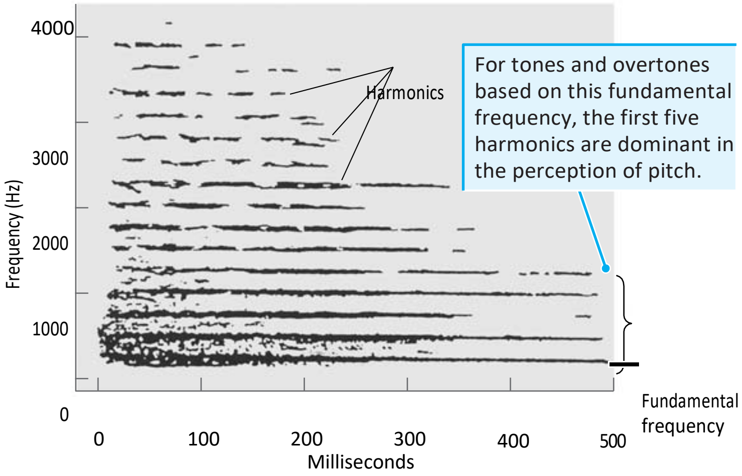
Music Perception

The second category of auditory deficit is in processing sounds related to music. Musical sounds may differ from one another in three aspects: loudness, timbre, and pitch.

- *Loudness* refers to the magnitude of a sensation as judged by a given person. Loudness, although related to the intensity of a sound as measured in decibels, is in fact a subjective evaluation described by such terms as "very loud," "soft," "very soft," and so forth.
- *Timbre* refers to the distinctive character of a sound, the quality by which it can be distinguished from all other sounds of similar pitch and loudness. For example, we can distinguish the sound of a violin from that of a trombone even though they may play the same note at the same loudness.
- *Pitch* refers to the position of a sound in a musical scale, as judged by the listener. Pitch is clearly related to frequency. Consider the note middle C, described as a pattern of sound frequencies as depicted in Figure 15.7. The amplitude of acoustic energy is conveyed by the darkness of the tracing in the figure. The lowest component of this note is the *fundamental frequency* of the sound pattern, which is 264 Hz, or middle C. The sound frequencies above the fundamental frequency are known as *overtones* or *partials.* The overtones are generally simple multiples of the fundamental (for example, 2 X 264, or 528 Hz; 4 X 264, or 1056 Hz), as can be seen in Figure 15.7. Those overtones that are multiples of the fundamental are known as *harmonics.*

The classic view, dating to Hermann Helmholtz in the late 1800s, held that pitch perception depends on the fundamental frequency, and the overtones provide timbre. This view now appears to be incorrect. If the fundamental frequency is removed from a note by means of electronic filters, the overtones are sufficient to determine the pitch of the fundamental frequency — a phenomenon known as *periodicity pitch.* The ability to determine pitch from the overtones alone is probably due to the fact that the difference between the frequencies of the various harmonics is equal to the fundamental frequency (for example, 792 Hz — 528 Hz = 264 Hz = the fundamental). The auditory system can determine this difference, and we perceive the fundamental frequency.

Figure 15.7 Spectrographic display of the steady-state part of middle C (264 Hz) played on a piano. Bands of acoustical energy are present at the fundamental frequency, as well as at integer multiples of the fundamental (harmonics). (After Ritsma, 1967.)



For tones and overtones based on this fundamental frequency, the first five harmonics are dominant in the perception of pitch.

The primary auditory cortex of the right temporal lobe appears to make this periodicity pitch discrimination. For example, Zatorre found that patients with right temporal lobectomies that include the primary auditory cortex are impaired at making pitch discriminations when the fundamental is absent but normal at making such discriminations when the fundamental is present. Right temporal lesions that spare the primary auditory cortex or left temporal lobectomies do not impair performance. Zatorre suggested that the right temporal lobe has a special function in extracting pitch from sound, regardless of whether the sound is speech or music. In regard to speech, the pitch will contribute to "tone" of voice, which is known as **prosody.**

Other aspects of music are also specially processed in the right temporal lobe. The simplest is the perception of timbre, which is impaired by right temporal lesions. In addition, more-complex aspects of music, such as scales, chords, and progressions, are all constructed from single musical notes. Although speculative, it seems likely that we humans develop a "musical store" much as we develop a "syntactic store" of words. Thus, when we encounter a musical scale or progression, we recognize it as such. The mechanism of such a hypothetical store is unknown, but it may be a function of the right auditory association cortex.

Finally, Liegeois-Chauval and colleagues point out that distinct musical processes may depend on specific cortical sites in the superior temporal gyrus (see Figure 15.2). Thus, in their study of patients with temporal lobectomies, these investigators found that rhythm discrimination was most affected by right posterior superior temporal gyrus damage, whereas distinguishing meter (for example, distinguishing a waltz and a march) was more affected by anterior damage to either temporal lobe.

Although it is tempting to compartmentalize music and language on opposite sides of the brain, it seems unlikely that the brain is specifically designed to treat them differently; rather, certain characteristics of musical and language input are probably analyzed selectively by the two hemispheres. Zatorre emphasized the key difference: the left hemisphere is concerned more with speed and the right hemisphere with distinguishing frequency differences, a process called *spectral sensitivity.*

Disorders of Music Perception

The fact that the brain appears to have neural networks dedicated to the processing of language and music leads to the conclusion that both language and music have biological roots. Although this conclusion seems obvious for language, it is less obvious for music, which has often been perceived as an artifact of culture. But considerable evidence suggests that humans are born with a predisposition for processing music.

Infants show learning preferences for musical scales and are biased toward perceiving the regularity (such as harmonics) on which music is built. Peretz argued that one of the strongest bits of evidence favoring the biological basis of music is that a surprising number of people have a condition known as *congenital amusia.* They are tone deaf. Apparently, amusic people have an abnormality in their neural networks for music, and no amount of training makes much difference. In fact, we have a colleague whose parents were both music teachers and, to the chagrin of her parents, she is amusic. She likes to note that she knows that the national anthem is being played because people stand up!

Liegeois-Chauvel and colleagues studied musical processing in a large group of patients with temporal lobectomies and found that injury to the right superior temporal gyrus impairs various aspects of processing necessary for discriminating melodies. In addition, a dissociation between the roles of the posterior and anterior regions of the superior temporal gyrus on different aspects of musical processing suggests their relative localization within the superior temporal gyrus.

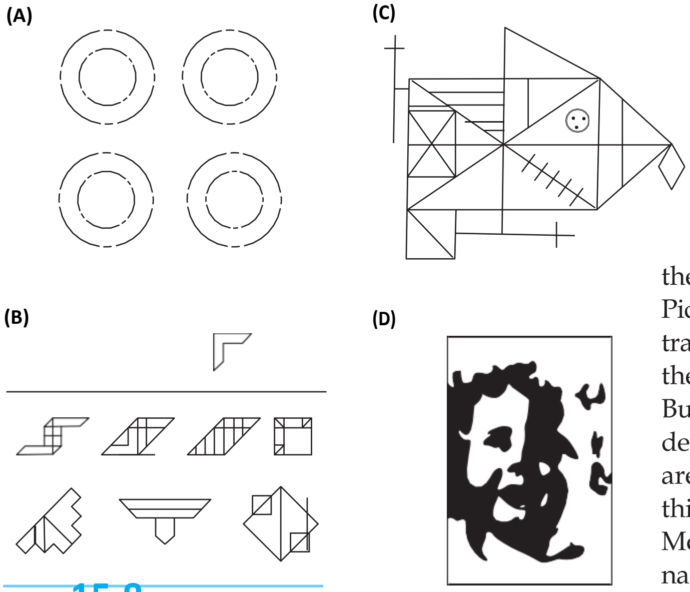


Figure 15.8 Tests for visual disorders. (A) Meier and French's test, in which the subject must identify the drawing that is different. (B) Sample of the Gottschaldt Hidden-Figures Test, in which the task is to detect and trace the sample (upper drawing) in each of the figures below it. (C) Rey Complex-Figure Test, in which the subject is asked to copy the drawing as exactly as possible. (D) Sample of the Mooney Closure Test, in which the task is to identify the face within the ambiguous shadows.

Disorders of Visual Perception

Although persons with temporal lobectomies do not normally have large defects in their visual fields, they do have deficits in visual perception. Such deficits were first demonstrated by Milner, who found that her patients with right temporal lobectomies were impaired in the interpretation of cartoon drawings in the McGill Picture-Anomalies Test. For example, one item illustrating a monkey in a cage features an oil painting on the wall of the cage—an obvious oddity or anomaly. But, although patients with right temporal lesions can describe the contents of the cartoon accurately, they are impaired at recognizing the anomalous aspects of this picture and others. Similarly, on a test such as the Mooney Closure Test or tests requiring the discrimination of complex patterns (Figure 15.8), patients with temporal-lobe damage perform very poorly.

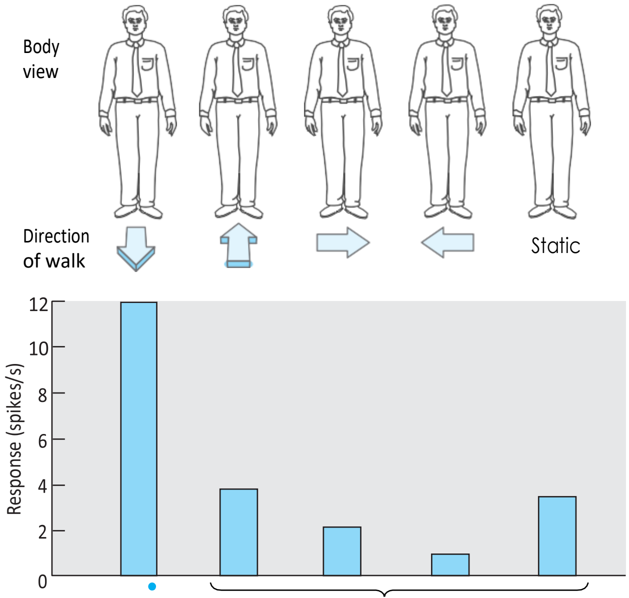
Facial Recognition and Biological Motion

One of the most interesting visual perceptual deficits is in facial perception and recognition. When one of us (B. K.) and his associates presented patients with the split-faces test (see Figure 13.17), they found that those with right temporal-lobe resections fail to show a bias for that part of the face falling in the left visual field, suggesting that these patients perceive faces abnormally. This conclusion is consistent with reports that patients with right temporal-lobe damage are impaired at the recognition and recall of faces or photographs of faces.

Furthermore, these patients do not appear able to perceive subtle social signals such as discreet but obvious glances at one's watch, a gesture often intended as a cue to break off a conversation. Presumably the patients fail to perceive the significance of the visual signal. Facial signals are a form of biological motion, the analysis of which we have seen to be a function of the temporal lobe.

The description of deficits in visual perception in people with temporal-lobe injury is consistent with the hypothetical role of the inferior temporal cortex in the ventral visual stream (see Chapter 13). An extensive literature shows that monkeys with inferior temporal lesions have severe and selective deficits in learning tasks that require the visual recognition of objects. Furthermore, inferior temporal cortex neurons in monkeys have long been known to have selective characteristics, such as a preference for faces or hands.

These preferences may be quite specific. For example, Perrett and colleagues showed that neurons in the superior temporal sulcus may be responsive to particular faces seen head-on, faces viewed in profile, posture of the head, or even particular facial expressions. More recently, Perrett also showed that some superior temporal sulcus cells are maximally sensitive to primate bodies that are moving in a particular direction, another characteristic biological motion (Figure 15.9). This finding is quite remarkable because the basic configuration of the stimulus is identical as the body moves in different directions; it is only the direction that changes.



STS neurons in the observing monkey respond more strongly to an approaching body...

...than to the same body moving in other directions or standing still.

Figure 15.9 Neuronal sensitivity to direction of body movements. (Top) Schematic representation of the front view of a body. (Bottom) The histogram illustrates a greater neuronal response of superior temporal sulcus (STS) neurons to the front view of a body that approaches the observing monkey compared with the same body views when the body is moving away to the right and to the left or is static. (After Perrett et al., 1990.)

Activation of Inferior Temporal Neurons

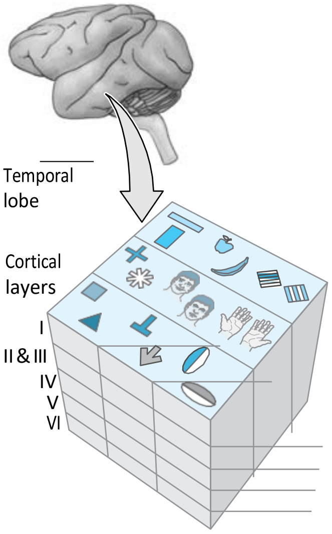
One problem with the identification of specialized temporal visual neurons is that the dedication of specific temporal cortex cells for every possible object feature in the world is impractical. Tanaka approached this problem by attempting to determine the features that are critical for activating neurons in the monkey inferior temporal cortex. He and his colleagues presented many three-dimensional animal and plant representations to find the effective stimuli for given cells. Then they tried to determine the necessary and sufficient properties of these cells.

Tanaka found that most cells in area TE require rather complex features for activation. These features contain a combination of characteristics such as orientation, size, color, and texture. Furthermore, as illustrated in Figure 15.10, he found that cells with similar, although slightly different, selectivity tend to cluster vertically in columns.

Organizationally, the cortex has an important vertical component (see Chapter 10), but the neurons organized in columns in the temporal cortex are not identical in their stimulus selectivity. Thus it seems likely that an object is not represented by the activity of a single cell but rather by the activity of many cells within a columnar module. This important finding provides an explanation for the phenomenon of stimulus equivalence—that is, the common observation that an object viewed at different orientations remains the same object. Tanaka speculates that the representation of objects by multiple cells in a columnar module in which the selectivity varies from cell to cell and effective stimuli largely overlap can provide a way for the brain to minimize the effect of small changes in input images.

Figure 15.10 Schematic representation of the columnar organization in area TE. Cells with similar but slightly different selectivity cluster in elongated vertical columns, perpendicular to the cortical surface.

Neurons in the temporal lobe form columns that respond to categories of shapes.



Tanaka and others have described two other remarkable features of inferior temporal neurons in monkeys. First, the stimulus specificity of these neurons is altered by experience. In a period of 1 year, monkeys were trained to discriminate 28 complex shapes. The stimulus preferences of inferior temporal neurons were then determined from a larger set of animal and plant models. In the trained monkeys, 39% of the inferior temporal neurons gave a maximum response to some of the stimuli used in training. This percentage compared with only 9% of the neurons in naive monkeys.

This result is exciting, because it shows that the temporal lobe's role in visual processing is not determined genetically but is subject to experience even in the adult. We can speculate that this experience-dependent characteristic allows the visual system to adapt to different demands in a changing visual environment. This feature is important for human visual recognition abilities that have very different demands in forests from those on open plains or in urban environments. In addition, experience-dependent visual neurons ensure that we can identify visual stimuli that were never encountered in the evolution of the human brain.

The second interesting feature of inferior temporal neurons is that they may not only process visual input but also provide a mechanism for the internal representation of the images of objects. Fuster and Jervey first demonstrated that, if monkeys are shown specific objects that are to be remembered, neurons in the monkey cortex continue to discharge during the "memory" period. These selective discharges of neurons may provide the basis of working memory for the stimuli. Furthermore, the discharges of these neurons may provide the basis for imagery. That is, the discharge of groups of neurons that are selective for characteristics of particular objects may provide a mental image of the object in its absence.

Disturbance of Selection of Visual and Auditory Input

We must select which inputs to process from the wealth of information in our environment. This selectivity is generally not conscious, because the nervous system automatically scans input and selectively perceives the environment. (Conscious control can be exerted, of course, as when you search for a mailbox to post a letter.)

Selectivity in auditory perception is best illustrated by the problem of listening to two conversations simultaneously. Because it is impossible to process the two competing inputs concurrently, the auditory system adopts one of two strategies: either one conversation is ignored or attention shifts back and forth from one conversation to the other. In either case, there is a selection of input. Selective perception in the visual system operates similarly. For example, because it is not possible to watch all floor events at a gymnastics meet simultaneously, either we focus our attention entirely on one event or shift it from one event to another.

Let us now consider the person with temporal-lobe damage. Selection of both auditory and visual input is impaired, which is ordinarily demonstrated only by special testing procedures. Selective attention to auditory input can be tested by dichotic listening (see Chapter 11). Recall that, when subjects are presented with two words simultaneously, one to each ear, normal subjects report more of the words presented to the right ear; if tonal sequences are presented dichotically, there will be a left-ear advantage.

This left-ear advantage is maintained in patients with temporal-lobe lesions, but left-temporal-lobe lesions result in an overall drop in the number of words recalled. One explanation for this effect is that the nervous system has difficulty focusing selectively on the input into one ear and attempts to process all the input concurrently; as a result, performance drops significantly.

Analogous findings are reported for visual input. If two different visual stimuli are presented simultaneously, one to each visual field, damage to the left temporal lobe impairs recall of content of the right visual field, but damage to the right temporal lobe impairs recall of content in *both* visual fields. Again, it may be that the nervous system is now unable to focus on distinctive features of the stimuli to allow efficient perception and storage of the input. In regard to visual input, however, it is noteworthy that right temporal lesions produce bilateral deficits, whereas left temporal lesions produce unilateral ones. This difference implies that the right temporal lobe may have a greater role than the left in selective attention to visual input.

Organization and Categorization

Asked to learn a list of words such as "dog, car, bus, apple, rat, lemon, cat, truck, orange," most of us will organize the words into three different categories—animals, vehicles, and fruit. If the list is later recalled, the items are likely to be recalled by category, and recall of the categories is likely to be used as an aid in recall of the items.

The ability to organize material is especially important for language and memory. For example, categorizing makes it possible to comprehend complex, extended sentences, including both the meaning of individual clauses and the information inferred from them. Organization of sensory input appears to be a function of the temporal lobes. Patients with left temporal lobectomies are impaired in their ability to categorize even single words or pictures of familiar objects.

Thus, patients have difficulty placing words or pictures into discrete categories, even when they are requested to, and they also have difficulty in using categories that most of us use automatically. For example, Milner has found that, when these patients are given a category name (such as animal) and are asked to recall exemplars of the category (such as dog, cat, rat), they have difficulty, even though they are fluent in other types of tests. Given that these patients have difficulty in simple types of categorization tasks studied in the laboratory, you can imagine that their difficulty in spontaneous organization may represent a significant deficit in cognition, especially in memory for complex material.

Neurolinguists propose that another type of categorization may take place in the left temporal lobe. Semantic categories are hierarchies of meaning in which a single word might belong to several categories simultaneously. For example, a duck belongs to the categories animal, bird, and waterfowl. Each of these categories is a refinement of the preceding one. Patients with posterior temporal lesions may show dysphasic symptoms in which they can recognize the broader categorization but have difficulty with the more specific ones.

Using Contextual Information

The meaning of identical stimuli can vary, depending on the context. For example, a word such as "fall" can refer to a season or to a tumble, depending on the context. Similarly, context may be a major cue for facial recognition. Most of us have encountered someone completely out of context (for example, while in Paris you encounter a clerk from your neighborhood store at home) and have been unable to recall who the person is until information about the context is provided.

A more complex example of extracting meaning from context is found in social situations. The interpretation of events, and indeed our role in events, depends on the social context. Thus, stimuli may be interpreted in one way when we are with our parents and in a different way when we are with our peers, an ability that is referred to as social cognition. (We return to social cognition in Chapter 22.) A simple example of the use of contextual information can be found in the McGill Picture-Anomalies Test described in the section on visual perceptual deficits. The only clue to the correct choice in the McGill anomalies is the context.

Memory

Interest in the temporal lobes' function in memory was stimulated in the early 1950s by the discovery that bilateral removal of the medial temporal lobes, including the hippocampus and amygdala, results in amnesia for all events after the surgery (**anterograde amnesia**). It is now clear that both the medial temporal regions and the temporal neocortex are important for memory functions (see Chapter 18).

Damage to the inferior temporal cortex specifically interferes with conscious recall of information, the extent of the memory disturbance increasing in direct proportion to the amount of temporal-lobe damaged. Lesions of the left temporal lobe result in impaired recall of verbal material, such as short stories and word lists, whether presented visually or aurally; lesions of the right temporal lobe result in impaired recall of nonverbal material, such as geometric drawings, faces, and tunes. Two case histories demonstrate the roles of the left and right temporal lobes in memory.

Mr. B., age 38, was suffering from an astrocytoma in the left temporal lobe. Before onset, he had been a successful executive in an oil company and was noted for his efficiency. As his tumor developed, he became forgetful, and at the time of hospital admission his efficiency had dropped drastically; he had begun to forget appointments and other important events. Forgetfulness had become such a problem that he had begun to write notes to himself to cover his memory problem, but he often mislaid the notes, leading to even greater embarrassment.

On formal tests of memory Mr. B. had special difficulty in recalling short stories read to him a few minutes earlier. In one test, he was read the following story from the Wechsler Memory Scale and was asked to repeat it as exactly as possible. "Anna Thompson of South Boston, employed as a scrub woman in an office building, was held up on State Street the night before and robbed of $15. She had four little children, the rent was due and they had not eaten for two days. The officers, touched by the woman's story, made up a purse for her."

Mr. B. recalled: "A woman was robbed and went to the police station where they made her a new purse. She had some children too." This performance is very poor for a person of Mr. B.'s intelligence and education. On the other hand, his immediate recall of digits was good; he could repeat strings of seven digits accurately. Similarly, his recall of geometric designs was within normal limits, illustrating the asymmetry of memory functions, because his right temporal lobe was intact.

Ms. C. illustrates the complement of Mr. B.'s syndrome. She was a bright 22-year-old college student who had an indolent tumor of the right temporal lobe. When we first saw her, after surgery, she complained of memory loss. She was within normal limits on formal tests of verbal memory, such as the story of Anna Thompson, but was seriously impaired on formal tests of visual memory, especially geometric drawings. For example, in one test she was shown geometric designs for 10 seconds and then asked to draw them from memory. Ten minutes later, she was asked to draw them again. She had difficulty with immediate recall (Figure 15.11) and, after 10 minutes, was unable to recall any of the drawings.

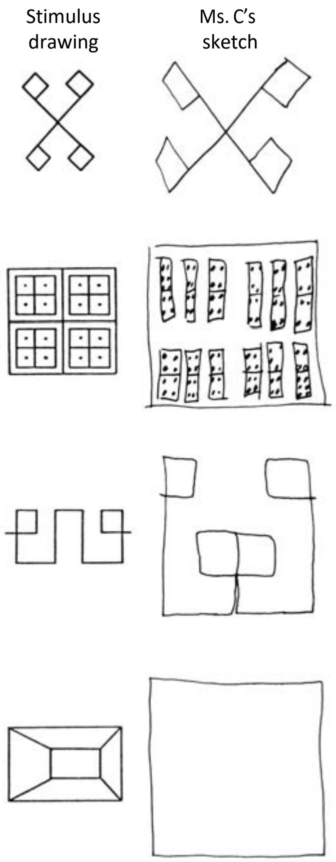


Figure 15.11 Impaired recall of geometric figures by Ms. C. In each set shown, the drawing at the left is the original stimulus and the drawing at the right is Ms. C.'s sketch made immediately after viewing each figure for 10 seconds. Note that Ms. C.'s impairment is worse with the more complex figures. Ms. C. was unable to recall even the simplest figure 10 minutes after viewing it.

Affect and Personality

Although temporal-lobe disorder has been associated with disturbance of affect in humans for nearly 100 years, knowledge about the details of this role is still surprisingly fragmentary. Wilder Penfield and others reported that stimulation of the anterior and medial temporal cortex produces feelings of fear, an effect also occasionally obtained from stimulating the amygdala. Recall, too, that H. H.'s wife complained that H. H.'s personality was different after his tumor and surgery from what it had been before.

Temporal-lobe epilepsy has traditionally been associated with personality characteristics that overemphasize trivia and the petty details of daily life. Pincus and Tucker described several symptoms of this personality, including pedantic speech, egocentricity, perseveration in discussions of personal problems (sometimes referred to as "stickiness," because one is stuck talking to the person), paranoia, preoccupation with religion, and proneness to aggressive outbursts. This constellation of behaviors produces what is described as *temporal-lobe personality*, although very few people combine all these traits.

Similar personality traits arise after temporal lobectomy. There appears to be a relative asymmetry in the symptoms, with right temporal lobectomy more likely to be associated with these personality traits than left temporal lobectomy. This observation has not been quantified, however, and warrants further study.

Clinical Neuropsychological Assessment of Temporal-Lobe Damage

A number of standardized assessment tools have proved sensitive and valid predictors of temporal-lobe injury (Table 15.2). Like the clinical neuropsychological tests of parietal-lobe function reviewed in Chapter 14, these tests do not assess all possible temporal-lobe symptoms, but it would be highly unusual for a person to perform normally on all these tests if there were damage to either temporal lobe.

- Auditory and visual processing capacity can be assessed by using dichotic listening and the McGill Picture-Anomalies Test. The picture-anomalies task is not as sensitive an indicator today as it was when first used in the 1950s, perhaps because video-based home entertainment has made the

Table 15.2 Standardized clinical neuropsychological tests for temporal-lobe damage

Function	Test	Basic reference
Auditory processing capacity	Dichotic words and melodies	Sparks et al., 1970
Visual processing capacity	McGill Picture Anomalies	Milner, 1958
Verbal memory	Revised Wechsler Memory Scale; logical stories and paired associates	Milner, 1975
Nonverbal memory	Rey Complex Figure	Taylor, 1969
Language	Token	de Renzi and Faglioni, 1978

average person more sophisticated visually. Nevertheless, a poor score on this test almost invariably denotes right temporal abnormality.

- The best test of general verbal memory ability is the revised Wechsler Memory Scale. However, because the Wechsler memory quotient is affected by nonspecific disorders of attention, two subtests—paired associates and logical stories—are often used as a purer measure of verbal memory capacity. The paired-associates subtest requires a subject to learn a series of word pairs (for example, north–south, cabbage–pen) such that, when one word is read (north, cabbage), its paired-associate word (south, pen) can be recalled. An example of the logical memory test was presented in reference to Mr. B.'s verbal memory defect.
- The Rey Complex-Figure Test has proved to be one of the best for evaluating nonverbal memory function of the right temporal lobe (see Figure 15.8C). A printed copy of a complex geometric pattern is placed before the subject with the instructions, "Copy the drawing as accurately as you can." Forty-five minutes later, the subject is asked to reproduce as much of the figure as he or she can remember. Although the scoring criteria provide an objective measure of nonverbal memory, the test has the drawback that depressed or poorly motivated subjects may perform poorly, not because of right temporal-lobe damage but because they refuse to try to recall the figure. There is no easy solution to this problem, because all tests of nonverbal memory are subject to this complication.
- A deficit in language comprehension could be the result of a lesion in any of the language zones of the left hemisphere (that is, in the parietal, temporal, or frontal lobes). No current neuropsychological assessment tool can localize the area of damage within the left hemisphere. For this reason, we once again recommend the token test as the test of choice for language comprehension.

Summary

The temporal lobe can be divided into four functional zones for auditory processes (superior temporal gyrus), visual processes (inferior temporal cortex), and the integration of these processes for emotion (amygdala) and spatial navigation and spatial and object memory (hippocampus and associated cortex).

The processing of auditory information is specialized for two characteristics: speed and frequency. Language processing requires analysis of rapid changes in sounds but, because people talk at different pitches (that is, high squeaky voices versus deep resonant voices), the understanding of language sounds can tolerate differences in frequencies. In contrast, music is relatively slower than language, but differences in frequency are critical. The left temporal lobe is more concerned with speed, whereas the right is more concerned with complex frequency patterns. Damage to the auditory regions of the temporal lobe produces deficits in the recognition of language (primarily left) and music (primarily right), as well as in sound localization.

The temporal lobe adds two features to both auditory and visual information—namely, tone (affect) and categorization. These aspects are important for understanding sensory input as well as for using it in biologically relevant ways, such as in biological motion. Whereas the parietal lobe processes spatial location with respect to movement, the temporal lobe uses spatial location as a feature of object recognition and in the development of memories for object location. Damage to the visual regions of the temporal lobe disrupt the recognition of complex visual stimuli, such as faces. Damage to medial temporal regions produces deficits in affect, personality, spatial navigation, and object memory.

Neuropsychological analyses of temporal-lobe functions utilize tests that are sensitive to discrete temporal-lobe injuries. Such tests include those of auditory processing (dichotic listening), visual processing (object recognition), memory (both verbal and nonverbal), and language.

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chapter 16

The Frontal Lobes

E. L. was a professor of botany at a college in upstate New York. Known for his organizational skills, E. L. had developed a large herbarium at the college and truly enjoyed having students working with him on various research projects. Late in the spring semester when he was 60 years old, E. L. began to have headaches and felt as if he had the flu; after a few days bed rest, however, he was not getting any better. He eventually visited his physician, who determined that E. L. had an infection, although the source was difficult to identify.

Meanwhile, E. L. began to develop cognitive symptoms that his wife found very worrisome. He seemed disorganized, showed little emotion, and, although a chapter of his unpublished book was due and he was never late in doing such things, he said that he just could not think of anything to write.

The most striking thing about E. L. when he arrived for his neuropsychological assessment was his flat affect and the virtual absence of facial expression—symptoms typical of left-frontal-lobe patients. This lack of affect was not associated with a lack of effort on the tests, however, because the assessment ranked his intelligence and general memory scores in the superior range. He did, nevertheless, register significant impairments on tests sensitive to frontal-lobe functions.

Talking with E. L. and his wife of more than 30 years made it clear that E. L. was having difficulty not only with his academic work but also with his social interactions with colleagues, friends, and his family. He found it difficult to interact even with close friends, and his wife was concerned that her husband was "not the man I married."

In a real sense, all neural roads eventually lead to the frontal lobes. As is apparent in E. L.'s case, when some of the roads lead nowhere, people can have major problems in generating appropriate behavior. In this chapter, we consider the anatomical organization of the frontal lobes, including the neural roads for information flow to and from them, before looking at a general theory of frontal-lobe function, the various symptoms associated with frontal-lobe injury, and diseases that affect the frontal lobes.

Anatomy of the Frontal Lobes

Children are notorious for their social faux pas because they do not recognize that the rules of behavior change with the social and environmental circumstances. Indeed, controlling our behavior in response to the social or environmental situation that we are in requires considerable skill, and we can all relate examples in which we goofed and behaved inappropriately. Fortunately, most of us do not err often, because our frontal lobes control our behavior with respect to time and place. Yet the frontal lobe can perform such a function only if it is provided with all the relevant sensory and mnemonic (that is, memory) information available.

Subdivisions of the Frontal Cortex

In the human brain, the frontal lobes comprise all the tissue in front of the central sulcus. This vast area, constituting 20% of the neocortex, is made up of several functionally distinct regions that we shall group into three general categories—motor, premotor, and prefrontal (Figures 16.1 and 16.2).

The motor cortex is area 4. The premotor cortex includes areas 6 and 8, which can be divided into four regions:

lateral area 6: premotor cortex

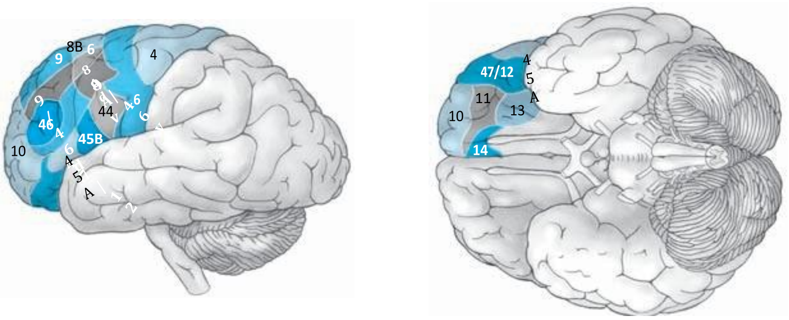
medial area 6: supplementary motor cortex

area 8: frontal eye field

area 8A: supplementary eye field

In humans, the lateral premotor area expanded as Broca's area (area 44) developed.

(A) Lateral view **(C) Ventral view**



(B) Medial view **(D) Functional zones**

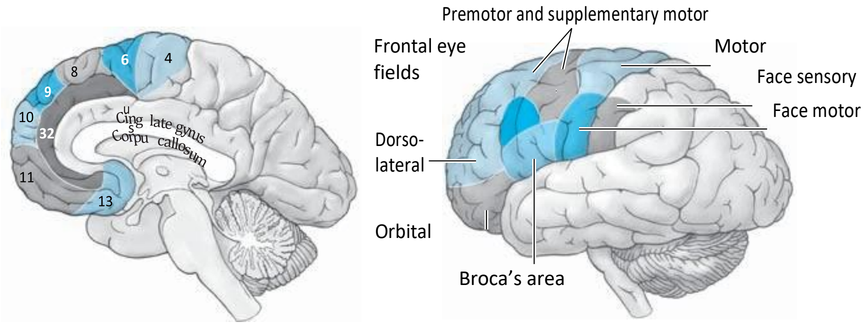


Figure 16.1 Petrides and Pandya's cytoarchitectonic map of the frontal lobe. Approximate boundaries of functional zones of the frontal lobe are shown in part D.

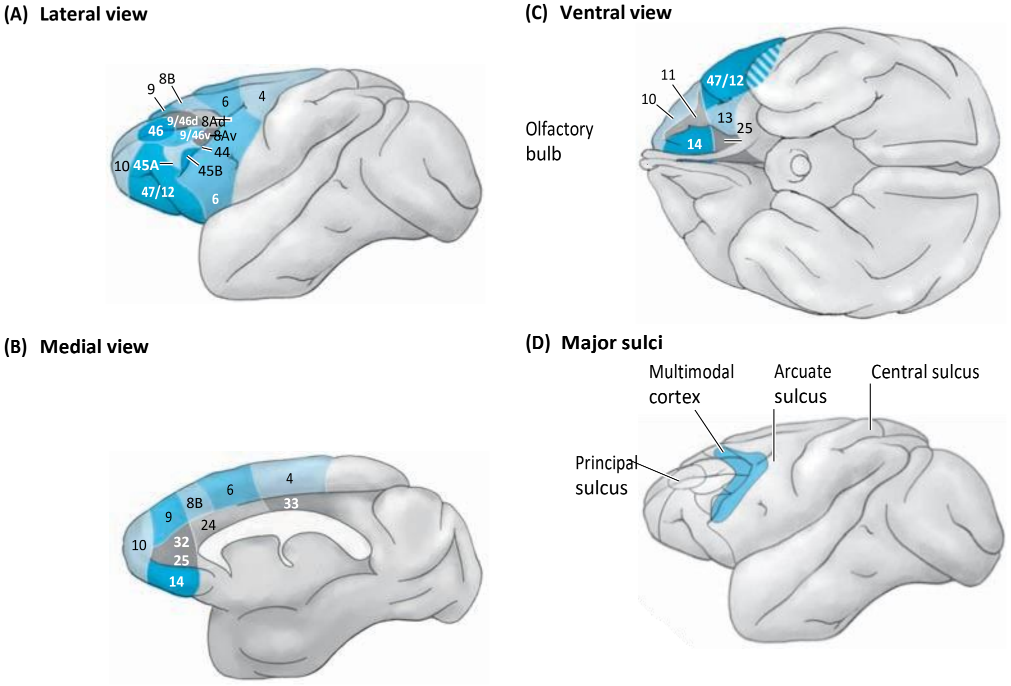


Figure 16.2 Petrides and Pandya's cytoarchitectonic map of the frontal lobe of the rhesus monkey. The two major sulci in the monkey frontal lobe are the principal sulcus and the arcuate sulcus, as shown in part D.

Prefrontal cortex is a peculiar name that derives from Jersey Rose and Clinton Woolsey's observation that the frontal lobes of all the mammalian species that they examined have a region that receives projections from the dorsomedial nucleus of the thalamus. They saw this thalamic projection as being parallel to the projections of the lateral and medial geniculate nuclei to the visual and the auditory cortex, respectively, and concluded that the dorsomedial projection could be used to define a similar region in different animal species. They termed this region the prefrontal cortex.

In primates, the prefrontal cortex can be divided into three regions (refer to Figures 16.1 and 16.2): (1) dorsolateral prefrontal cortex (areas 9 and 46); (2) inferior (ventral) prefrontal cortex (areas 11, 12, 13, and 14); and (3) medial frontal cortex (areas 25 and 32). The inferior frontal cortex is sometimes referred to as the **orbital frontal cortex** because of its relation to the orbit (eye socket). The medial frontal area is sometimes considered part of the anterior cingulate region rather than part of the prefrontal cortex, even though it may receive dorsomedial projections.

As in the temporal lobe, many areas in the frontal lobe are multimodal. Cells responsive to combinations of visual, auditory, and somatic stimuli are found in the lateral premotor cortex (area 6) and in area 46. In contrast, cells responsive to taste and olfaction are found in area 13. The latter cells likely produce our perception of flavor in foods.

Connections of the Motor and Premotor Areas

The motor and premotor areas are part of a functional system to control movements directly. Several groups of connections bind up this system:

- The motor cortex projects to the spinal motor neurons to control limb, hand, foot, and digit movements and to the appropriate cranial nerve motor neurons to control facial movements. It also projects to other motor structures such as the basal ganglia and the red nucleus.

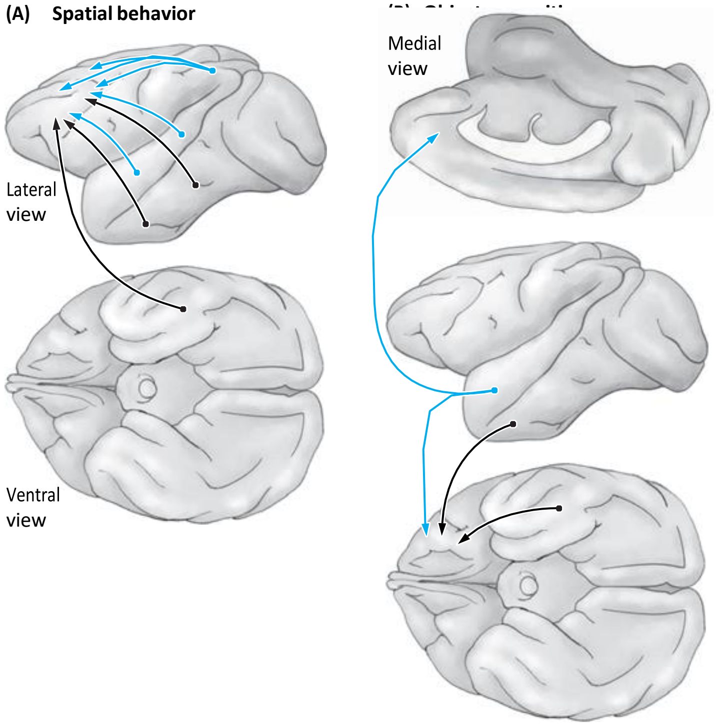
- The premotor areas can influence movement directly through corticospinal projections or indirectly through projections to the motor cortex. The premotor regions also receive projections from the posterior parietal areas PE and PF. Thus, the premotor regions are connected to areas concerned with the execution of limb movements.
- The frontal eye fields (areas 8 and 8A) receive projections from regions controlling eye movements and send projections to these regions. Thus, these regions receive visual input from posterior parietal region PG and the superior colliculus.
- All premotor areas receive projections from the dorsolateral prefrontal cortex, which implies that this prefrontal area has some role in the control of limb and eye movements.

Figure 16.3 The corticocortical connections to the frontal lobe of the rhesus monkey (see Figure 16.2). (A) The connections to the dorsolateral surface include projections from posterior parietal as well as temporal regions. (B) The connections to the inferior frontal region are from the temporal lobe. Connections from the insula and olfactory cortex are not shown.

Connections of the Prefrontal Areas

The prefrontal areas can be viewed as the end points of the dorsal (object recognition) and ventral (spatial behavior) visual streams. In fact, Felleman and van Essen included prefrontal regions as part of the visual cortex (see Figure 10.19).

The dorsolateral prefrontal cortex (areas 9 and 46) receives its main inputs from the posterior parietal areas and the superior temporal sulcus. These connections are reciprocal. In addition, the dorsolateral cortex has extensive connections to regions to which the posterior parietal cortex also projects, including the cingulate cortex, basal ganglia, and superior colliculus (see Figure 14.2). The key to understanding the functions of the dorsolateral cortex lies in its relation to the posterior parietal cortex (Figure 16.3A).



The orbital frontal cortex (areas 11 through 14) receives its main afferents from the temporal lobe, including the auditory regions of the superior temporal gyrus, the visual regions of TE and the superior temporal sulcus, and the amygdala (Figure 16.3B). In addition, there are connections from the somatosensory cortex (area 43), gustatory cortex (in the insula), and olfactory regions of the pyriform cortex, as illustrated in Figure 16.4. The orbital cortex therefore gains input from all sensory modalities. The orbital frontal area projects subcortically to the amygdala and hypothalamus, providing a route for influencing the autonomic system, which controls changes in blood pressure, respiration, and so on. These physiological changes are important in emotional responses.

The prefrontal regions receive significant input from dopaminergic cells in the tegmentum. This modulatory input plays an important role in regulating how prefrontal neurons react to stimuli, including stressful stimuli, and probably plays some role in our different emotional states. Abnormalities in this projection play a central role in schizophrenia.

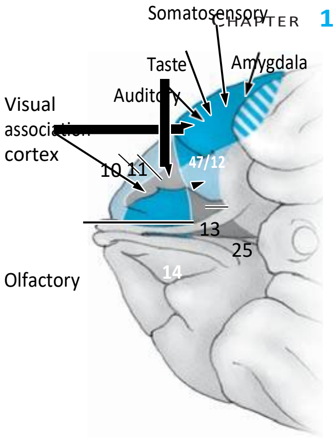


Figure 16.4 Inputs to the orbitofrontal cortex. Schematic illustration of the ventral surface of the monkey orbitofrontal cortex, including inputs from all sensory regions. (After Rolls, 1998.)

A Theory of Frontal-Lobe Function

Imagine the following scenario. At the last moment, you have invited friends for dinner. Because you have nothing to serve, you must go shopping after you leave work at 5:00 P.M. Before leaving, you prepare a list of items to buy. You are working under a time constraint because you must return home before your guests arrive and you need time to prepare. Because the items you need are not all at the same store, you must make an efficient plan of travel. You also must not be distracted by stores selling items (such as shoes) that you do not need or by extended chats with store clerks or friends whom you might encounter.

The task that you have set yourself is a bit rushed, but for most people it offers little challenge. People with frontal-lobe injury, however, cannot manage it. The fundamental requirements of the task that challenge frontal-lobe patients are as follows:

- Planning in advance and selecting from many options
- Ignoring extraneous stimuli and persisting in the task at hand
- Keeping track of the stores to which they have gone and the items that they have already purchased

The behavioral requirements of this task can be described as the temporal organization of behavior, and this organization is the general function of the frontal lobe. Thus, the frontal lobe contains control systems that implement different behavioral strategies in response to both internal and external cues. In recent years, it has become fashionable to refer to these temporal systems as *executive functions,* although we do not want to read too much into this label. The premotor and prefrontal regions contribute in different ways to this control function, and so we will consider them separately.

Functions of the Premotor Cortex

Whereas the motor cortex provides a mechanism for the execution of individual movements, the premotor cortex selects the movements to be executed. Consider the behavior of a resting dog. It may get up and respond to its owner's call or it may get up for no apparent reason and wander about the yard.

The former movements are made in response to a specific environmental cue, whereas the latter behavior can be regarded as a response to an internal event. Passingham suggested that the premotor region functions primarily to choose behavior in response to external cues and the supplementary motor region makes a greater internal contribution when no such cues are available.

Just as we choose limb movements, we must select eye movements. This selection is the function of the frontal eye fields. Like limb movements, eye movements can be made to specific targets that are visible or they can be made on the basis of internal cues. Thus, we can make eye movements to look at specific objects or we can gaze around, seemingly without purpose. Passingham suggested that area 8 is specialized for stimulus-directed movements, whereas area 8A is responsible for internally driven movements.

The role of the premotor cortex in response selection was first shown in normal subjects by Roland and his colleagues. They compared the cerebral blood flow in subjects making either a repetitive movement of one finger or a complex sequence of 16 movements of the fingers of one hand. The increase in blood flow in the supplementary motor cortexes *in both hemispheres* was larger in the sequence task than in the repetitive task. There was, however, no increase in blood flow in the premotor region.

Roland concluded that the supplementary motor region plays a special role in the selection and direction of motor sequences. An important aspect of Roland's experiment is that there was no external cue for the movements. That is, the production of the movement sequence was self-paced, or internally driven.

Deiber and colleagues showed that the premotor cortex is activated when movement sequences are paced externally by a cue. In their experiment, the subjects performed one of two tasks. In the first task, whenever a tone sounded, they made a fixed movement, which was to move a joystick forward. In this case, there was no response selection; the same response was made each time. In the second task, when the subjects heard the tone, they randomly made one of four movements of the joystick (forward, backward, left, or right). This task required a choice of movement. The results showed a significant effect of response selection: there was an increase in blood flow to both premotor areas in the choice condition relative to the fixed condition.

It is curious that both premotor regions were activated in the Deiber task, but an experiment by Jenkins and colleagues may provide an explanation. These researchers compared the performance of a prelearned sequence of finger movements with the learning of a sequence in which a tone indicated whether the sequence was correct or incorrect. The medial region was relatively more activated during the prelearned sequence, and the lateral region was more activated during the learning sequence. It seems likely that, during the prelearned movement, the cues were internal, whereas, on the learning task, the subjects had to attend to external cues.

Functions of the Prefrontal Cortex

The motor cortex is responsible for making movements. The premotor cortex selects movements. The prefrontal cortex controls cognitive processes so that appropriate movements are selected at the correct time and place. This selection may be controlled by internalized information or external cues or it may be made in response to context or self-knowledge. We consider these aspects separately.

Internal Cues

The internalized record of what has just taken place is independent of the existing sensory information and can be called *temporal memory, working memory,* or *short-term memory.* We use **temporal memory** here to refer to a neural record of recent events and their order. These events may be related to things or to movements and thus derive their information from the object-recognition or motor streams of sensory processing.

Recall that both streams project to the prefrontal cortex, although to different places (see Figure 16.3), which suggests temporal memory for both motor and object information, although the memory will be localized in different places in the frontal cortex. The dorsolateral areas are especially engaged in the selection of behavior based on temporal memory.

External Cues

People whose temporal memory is defective become dependent on environmental cues to determine their behavior. That is, behavior is not under the control of internalized knowledge but is controlled directly by external cues. One effect of this condition is that people with frontal-lobe injuries have difficulty in inhibiting behavior directed to external stimuli. In our dinner-party example, frontal-lobe patients would enter a shoe store or chat with friends as they responded to environmental cues that they encountered. (We have probably all experienced occasions when the temporal organization of our behavior failed and we were controlled by external cues rather than internalized information. How many times have you started to do something, been distracted by a question or event, and then been unable to recall what you were going to do? Sadly, this phenomenon increases with age, which is not reassuring information about the state of one's prefrontal cortex.)

One type of environmental cue is feedback about the rewarding properties of stimuli. For example, if you imagine that a certain stimulus, such as a photograph of your grandmother, is always associated with a reward, such as wonderful food, then you learn the association between the visual stimulus (the photograph of grandma) and the reinforcement (food). The learning of such associations is central to much of what we do as we learn about the world, and the orbital cortex is central to learning by associations.

Context Cues

We humans live complex lives. We live in social groups in which we have multiple simultaneous roles as children, parents, friends, siblings, lovers, workers, and so on. Each of these roles is governed by rules of behavior that we are expected to follow: our behavior around our grandparents is certainly different from our behavior with our high-school friends. Similarly, our behavior varies with the environment: we are quiet at a movie theater or in a library, but we may be noisy at a football game or at a picnic.

Behavior, then, is context dependent. Hence, behavior that is appropriate at one moment may not be appropriate if there are subtle changes in the context. This point is beautifully illustrated in Jane Goodall's graphic descriptions of the different behavioral patterns exhibited by chimpanzees. The makeup of the social group at any given time dictates the behavior of each chimpanzee. Given the presence and position of certain animals, a particular chimp may be bold and relaxed, whereas, with a different group of animals, the chimp is quiet and nervous. Further, an error in evaluating the context can have grievous consequences.

It may be no accident that the frontal lobe has grown so large in primates that are highly social. We can easily see the importance of social context when we reflect on our behavior with our grandparents versus that with our closest friends. It is common experience that our tone of voice, the use of slang or swear words, and the content of conversations are quite different in the two contexts.

The choice of behaviors in context requires detailed sensory information, which is conveyed to the inferior frontal cortex from the temporal lobe. Context also means affective context, and this contribution comes from the amygdala. People with orbital frontal lesions, which are common in closed-head injuries (damage that results from a blow to the head), have difficulty with context, especially in social situations, and are notorious for making social gaffes. Closed-head injuries are considered in detail in Chapter 26.

Autonoetic Awareness

Not only is our behavior under the control of ongoing sensory input, temporal memory, and context, but it is also affected by a lifetime of experiences and goals. Tulving called this autobiographical knowledge **autonoetic awareness** (that is, self-knowing). Tulving's idea is that autonoetic awareness makes it possible to bind together the awareness of oneself as a continuous entity through time.

Impairment in autonoetic awareness results in a deficit in the self-regulation of behavior. Thus, our behavior is under the influence of our personal past experiences and life goals for the future such that we interpret the world in our daily life within our own frames of reference. Patients with orbital frontal injury often lose this self-knowledge and have real difficulty in daily living. Levine and colleagues described M. L., a salesman whose orbital frontal injury resulted from a closed-head injury. M. L. noted that maintaining a close relation with his wife of 10 years was very difficult. "I have a hard time relating to my wife. I don't know why I married this person. I told myself I must have been happy, and they said I was." This type of symptom surely would be very disruptive to daily living, but it is not easy to capture with a neuropsychological test, in part because the symptoms are so individual.

Asymmetry of Frontal-Lobe Function

In keeping with the general complementary organization of the left and right hemispheres, as a rule the left frontal lobe has a preferential role in language-related movements, including speech, whereas the right frontal lobe plays a greater role in nonverbal movements such as facial expression. Like the asymmetry of the parietal and temporal lobes, the asymmetry of frontal-lobe function is relative rather than absolute; the results of studies of patients with frontal lesions indicate that both frontal lobes play a role in nearly all behavior. Thus, the laterality of function disturbed by frontal-

Table 16.1 Relative frequency of defective performance on neuropsychological tests

	PERCENTAGE OF GROUP SHOWING A DEFICIT		
Test	**Left hemisphere (%)**	**Right hemisphere (%)**	**Bilateral (%)**
Verbal fluency	70	38	71
Verbal learning	30	13	86
Block construction	10	50	43
Design copying	10	38	43
Time orientation	0	0	57
Proverbs	20	25	71

Source: After Benton, 1968.

lobe lesions is far less striking than that observed from lesions in the more-posterior lobes.

Nonetheless, as with the temporal lobe, there is reason to believe that some effects of bifrontal lesions cannot be duplicated by lesions of either hemisphere alone. Table 16.1 summarizes a study comparing the behavioral effects of unilateral and bilateral frontal lesions. People with bifrontal lesions are severely impaired in reporting the time of day and in decoding proverbs, effects seldom seen subsequent to unilateral frontal lesions.

Recently, Tulving and his colleagues proposed that the left and right frontal lobes may play different roles in memory processing: the left prefrontal cortex is proposed to be have a greater role in encoding information into memory, whereas the right prefrontal cortex is more engaged than the left in retrieval. This hypothesis remains controversial, in part because it is difficult to fit such a finding with our notions of what cerebral asymmetry represents. We shall return to the Tulving proposal in Chapter 18 (for a review, see Lepage et al., 2000, and Tulving, 2002).

Heterogeneity of Frontal-Lobe Function

Shallice and Burgess noted that correlations among performance on tasks sensitive to frontal-lobe injury are relatively low. Among the many explanations offered for low interest correlations, one is that the tests require different cognitive operations for their successful solution. These different functions require different bits of the frontal lobe, and, given that the exact site of injury will vary among patients, the different tests are impaired to different degrees.

Thus, as we consider the different symptoms of frontal-lobe injury, we must remember that any individual patient is unlikely to show all the symptoms, and the severity of symptoms will vary with lesion location. Few imaging studies have addressed the matter of heterogeneity and, as we shall see, the trend has been for evidence favoring homogeneity of function. The Snapshot on page 401 shows, however, that, at least in the orbital frontal cortex, there is evidence of discrete localization of functions.

Symptoms of Frontal-Lobe Lesions

Of primary concern here are the effects of unilateral lesions to the frontal cortex. In an effort to organize the symptoms conceptually, we have grouped them into eight major categories (Table 16.2). We do not mean to imply that the brain respects these categories but rather that the categories provide a conceptual framework within which to consider the symptoms.

Disturbances of Motor Function

Frontal lesions can impair a person's ability to make a wide variety of movements, to order movement sequences, and even to speak.

Fine Movements, Speed, and Strength

Damage to the primary motor cortex is typically associated with a chronic loss of the ability to make fine, independent finger movements, presumably owing to a loss of direct corticospinal projections onto motor neurons. In addition, there is a loss of speed and strength in both hand and limb movements in the contralateral limbs. The loss of strength is not merely a symptom of damage to area 4, because lesions restricted to the prefrontal cortex also lead to a reduction in hand strength.

Movement Programming

In a classic paper in 1950, Karl Lashley asked how movements are put together in a particular order. How is it, he asked, that a violinist can play an arpeggio so quickly and flawlessly? Clearly, each note is not "thought of" separately. And how is it that, in a tennis game, a player can make very rapid movements, seemingly much too fast to have considered each movement by itself?

Lashley presumed that this function—serially ordering complex chains of behavior in relation to varying stimuli—must somehow be a function of the neocortex. Although he believed it to be a function of the entire neocortex, it appears more likely to be a function of the frontal lobes. Removal of the supplementary motor cortex results in a transient disruption of nearly all voluntary movements (including speech, if the removal is on the left). There is rapid recovery, however, and the only permanent disability appears to be in the performance of rapidly alternating movements with the hands or fingers.

The likely reason that relatively minor symptoms result from rather large supplementary motor lesions is that both the left and the right premotor cortexes participate in the control of movement. This idea is supported by observations that both left and right premotor areas show an increase in blood flow during unimanual tasks in humans; in monkeys, cells in both the left and the right areas show increased activity regardless of which hand is moving. There is also a bilateral projection from each supplementary motor cortex to the basal ganglia.

Further evidence favoring a role for the frontal cortex in movement programming comes from the results of a study by Kolb and Milner, in which patients with localized unilateral frontal lobectomies (most of which did not include the premotor cortex) were asked to copy a series of arm or facial movements (see Figure 14.8). Although the patients showed mild impairment in copying the arm

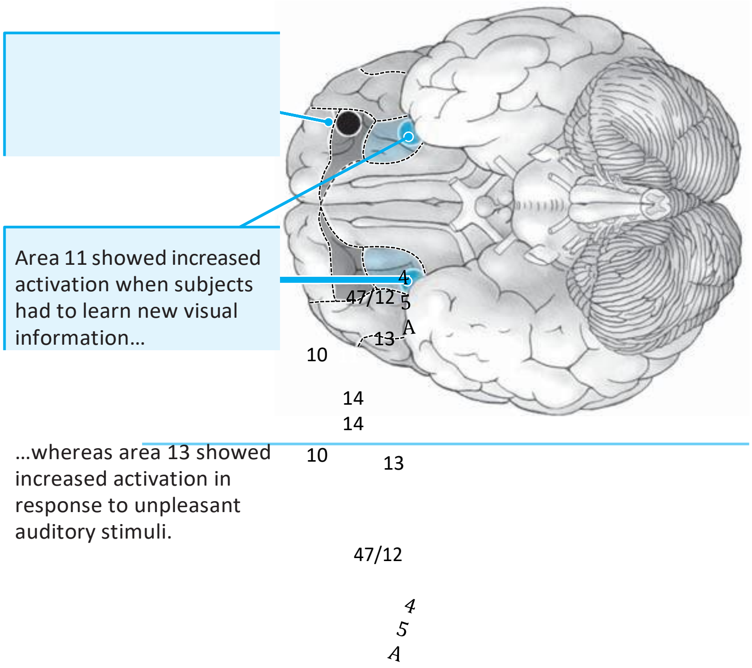
S N A P S H O T

Heterogeneity of Function in the Orbital Frontal Cortex

The orbital frontal cortex is a large region of the frontal lobe that includes at least five subregions—namely, Brodmann's areas 10 through 14. Different regions have different patterns of connectivity. Area 13, for example, has extensive connections with the amygdala and hypothalamus, whereas area 11 has connections with medial temporal cortical areas taking part in recognition memory.

The orbital frontal cortex is a challenge to study functionally in the laboratory because its location makes discrete lesions difficult to produce. Furthermore, although the orbital frontal cortex is often affected in closed-head injuries, these injuries are not focal but tend to be diffuse across the orbital region.

Frey and Petrides examined functional heterogeneity in the orbital region in two parallel PET studies. In one study, subjects heard either the sounds of violent car crashes, which they suspected would be perceived as unpleasant, or familiar abstract sounds generated from an electronic keyboard. In the other study, the subjects were presented with novel abstract visual designs that they had to either commit to memory or just view. Abstract designs were used to prevent subjects from verbalizing the images and thus provoking semantic associations.


Area 11 showed increased activation when subjects had to learn new visual information...

...whereas area 13 showed increased activation in response to unpleasant auditory stimuli.

Activation of the orbital frontal cortex by sensory stimulation. (After Frey and Petrides, 2000, and Frey, Kostopoulous, and Petrides, 2000.)

As shown in the adjoining figure, area 13 showed increased activation in response to the unpleasant auditory stimuli, whereas area 11 showed increased activation when subjects had to learn new visual information. These results show a clear functional dissociation of the two orbital regions: area 13 (richly connected to the amygdala and hypothalamus) processes unpleasant auditory information; area 11 (medial temporal cortical connections) processes the encoding of new visual information.

Area 13 can be seen as a region that can alert an organism to attend to stimuli that have affective qualities. We might predict that people with damage to area 13 would be less responsive to threatening stimuli, and they are. It would be interesting to determine whether both areas would be implicated if unpleasant stimuli were to be encoded.

(After S. Frey and M. Petrides. Orbitofrontal cortex: A key prefrontal region for encoding information. *Proceedings of the National Academy of Sciences of the United States of America* 97:8723–8727, 2000; S. Frey, P. Kostopoulous, and M. Petrides. Orbitofrontal involvement in the processing of unpleasant auditory information. *European Journal of Neuroscience* 12:3709–3712, 2000.)

movements, it was small compared with the performance of patients with left-parietal-lobe lesions. In contrast, patients with both left- and right-frontal-lobe damage were very poor at copying a series of facial movements.

An analysis of the facial-movement task showed that the groups with frontal-lobe lesions made more errors of sequence than did normal controls or other groups of patients. In other words, patients with frontal-lobe lesions had

Table 16.2 Summary of major symptoms of frontal-lobe damage

Most probable symptom	Lesion site	Basic reference
Disturbances of Motor Function		
Loss of fine movements	Area 4	Kuypers, 1981
Loss of strength	Areas 4 and 6; dorsolateral	Leonard et al., 1988
Poor movement programming	Premotor Dorsolateral	Roland et al., 1980 Kolb and Milner, 1981
Poor voluntary eye gaze	Frontal eye fields	Guitton et al., 1982
Poor corollary discharge	Dorsolateral, premotor	Teuber, 1964
Broca's aphasia	Area 44	Brown, 1972
Loss of Divergent Thinking		
Reduced spontaneity	Orbital	Jones-Gotman and Milner, 1977
Poor strategy formation	Dorsolateral?	Shallice, 1988
Poor frequency estimate	Dorsolateral	Smith and Milner, 1984
Environmental Control of Behavior		
Poor response inhibition	Prefrontal	Milner, 1964
Impaired associative learning	Dorsolateral	Petrides, 1997
Risk taking and rule breaking	Prefrontal	Miller, 1985
Gambling	Orbital	Bechara et al., 2000
Self-regulatory disorder	Orbital	Levine et al., 1998
Poor Temporal Memory		
Poor working memory	Dorsolateral	Petrides, 2000
Poor delayed response	Dorsolateral	Freedman and Oscar-Berman, 1986a
Other Symptoms		
Impaired social behavior	Orbital; dorsolateral	Blumer and Benson, 1975
Altered sexual behavior	Orbital	Walker and Blumer, 1975
Impaired olfactory discrimination	Orbital	Jones-Gotman and Zatorre, 1993
Disorders associated with damage to the facial area	Face	Taylor, 1979

difficulty ordering the various components of the sequence into a chain of movements. The components were recalled correctly but in the wrong order. To be sure, these patients made other sorts of errors as well, especially errors of memory in which items were not recalled. The reproduction of movement sequences requires temporal memory, and our impression is that the largest deficits come from dorsolateral lesions.

The observation that frontal injury severely disrupts the copying of facial but not arm movements implies that the frontal lobe may play a special role in the control of the face, perhaps even including the tongue. We shall see in the next section that patients with frontal-lobe damage exhibit relatively little spontaneous facial expression—a result in accordance with the possible special role of the frontal lobe in the control of the face.

Voluntary Gaze

A number of studies using quite different procedures have been reported in which frontal-lobe lesions produce alterations in voluntary eye gaze. For example, Teuber presented patients with an array of 48 patterns on a screen. The patterns could be distinguished by shape or color or both (Figure 16.5). At a warning signal, a duplicate of one of the 48 patterns appeared in the center of the array, and the subject's task was to identify the matching pattern by pointing to it. Patients with frontal-lobe lesions were impaired at finding the duplicate pattern.

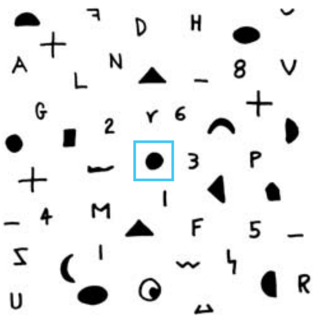


Figure 16.5 Visual search task used by Teuber. The subject must locate a duplicate of the shape inside the central box by pointing to it. (After Teuber, 1964.)

Luria recorded patients' eye movements as they examined a picture of a complex scene. The eye-movement patterns of the patients with large frontal-lobe lesions were quite different from those of normal control subjects or those of patients with more-posterior lesions. For example, if a normal control was asked about the age of the people in a picture, his or her eyes fixed on the heads; if asked how they are dressed, the eyes fixed on the clothing. Patients with large frontal-lobe lesions tended to glance over the picture more or less at random, and a change in the question about the picture failed to alter the direction or the pattern of eye movements. Visual search in Luria's task would require internalized knowledge to direct the eyes.

Guitton and his colleagues examined a different type of oculomotor defect in frontal-lobe patients. They studied the ability of patients to make voluntary eye movements toward or away from briefly appearing targets presented at random to the right or the left of a fixation point. Normally, if a stimulus cue is presented briefly in either visual field, a person will make a quick eye movement (a saccade) toward the stimulus.

Patients with frontal-lobe lesions had no difficulty doing so, and so Guitton and his coworkers added a second feature to the task. Rather than making eye movements toward a target, the patients had to move their eyes to the same place in the opposite visual field. The task therefore required inhibition of the normal saccade and a voluntary saccade toward a similar point in the opposite direction.

Patients with frontal lesions had two deficits on this variation of the task. First, although normal subjects failed to inhibit a short-latency response toward the cue in about 20% of the trials, patients with frontal lesions had much more difficulty. Second, after the initial saccade in the incorrect direction, normal subjects had no difficulty in making a large corrective saccade toward the opposite field. In contrast, patients with frontal lesions, which included the frontal eye fields, had difficulty in executing the corrective response when the response had to be generated by the damaged hemisphere. In other words, they had difficulty in moving the eyes to the field contralateral to the frontal lesion. Corrective movements could be made normally in the field on the same side as the lesion.

The difficulty that patients with frontal lesions encounter in the visual-search task and in the saccade task indicates the importance of the frontal cortex for certain aspects of oculomotor control. Only the study by Guitton and associates localized the effect in the frontal eye fields, but it is likely that the most severe deficits in performing such tasks are associated with damage to those fields.

Corollary Discharge

If you push on your eyeball, the world appears to move. If you move your eyes, the world remains stable. Why? Teuber proposed that, for a movement to take place, a neural signal must produce the movement as well as a signal that the movement is going to take place. If the eyes are moved mechanically, there is no such signal and the world moves. However, when you move your eyes, there is a neural signal that movement will happen and the world stays still. This signal has been termed **corollary discharge** or **reafference.**

Teuber argued that voluntary movements require two sets of signals rather than one. A movement command, through the motor system, effects the movements, and a signal (corollary discharge) from the frontal lobe to the parietal and temporal association cortex presets the sensory system to anticipate the motor act. Thus, a person's sensory system can interpret changes in the external world in light of information about his or her movement. For example, when you are running, the external world remains stable even though your sense organs are in motion, because the corollary discharge from the frontal lobe to the parietotemporal cortex signals that the movements are taking place. A frontal lesion therefore can not only disturb the production of a movement but also interfere with the message to the rest of the brain that a movement is taking place. By this indirect means, perception of the world by the posterior association cortex is altered.

One source of evidence that the frontal lobe plays a role in corollary discharge comes from the results of studies of cells in the frontal eye fields. Bizzi and Schiller, among others, found that some cells in the frontal eye fields fire simultaneously with movements of the eyes. These cells cannot be causing the eyes to move, because to do so they would have to fire before the eye movements (just as to accelerate an automobile, you must first depress the gas pedal). Rather, these cells must be monitoring the ongoing movement—a process suspiciously similar to what would be expected from a region controlling corollary discharge.

Speech

Speech is an example of movement selection. Passingham suggested that words are responses generated in the context of both internal and external stimuli. If the frontal lobe has a mechanism for selecting responses, then it must select words, too. The frontal lobe contains two speech zones: Broca's area, which can be regarded as an extension of the lateral premotor area, and the supplementary speech area, which may be an extension of the supplementary motor area (see Figure 16.1D).

Viewed in this way, Broca's area has a critical role when a word must be retrieved on the basis of an object, word, letter, or meaning. That is, like the premotor area's role in other behaviors, Broca's area selects words on the basis of cues. In contrast, the supplementary speech area is required to retrieve words without external cues, which also is consistent with the general function of the supplementary motor area.

People with strokes in Broca's area are impaired in their ability to use verbs and to produce appropriate grammar, a symptom known as agrammatism. People with strokes that include the supplementary speech area and extend into the left medial frontal region are often mute. The ability to speak usually returns after a few weeks in people with unilateral lesions but not in those with bilateral lesions. This outcome again supports the bilateral participation of the supplementary motor areas in movement selection. The role of the supplementary motor region is corroborated by the results of blood-flow studies done by Roland, who showed activation of the medial premotor area when subjects recall the months of the year, which is done without external cues.

Loss of Divergent Thinking

One of the clearest differences between the effects of parietal- and temporal-lobe lesions and the effects of frontal-lobe lesions is in performance on standard intelligence tests. Posterior lesions produce reliable, and often large, decreases in IQ scores, but frontal lesions do not. The puzzle is why patients with frontal-lobe damage appear to do such "stupid" things.

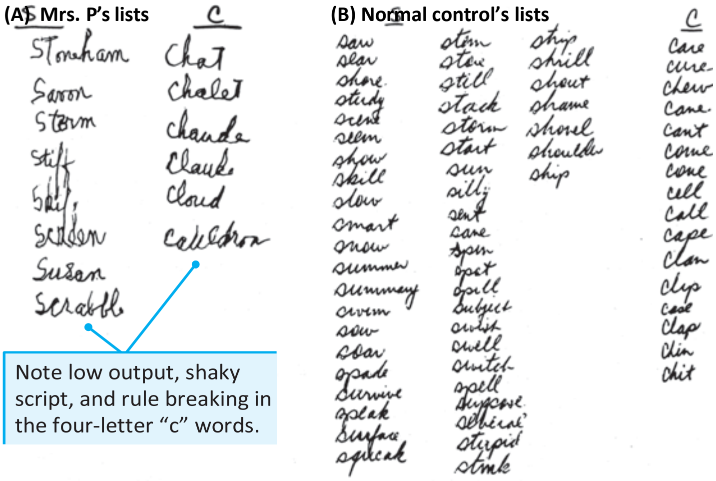
Guilford noted that traditional intelligence tests appear to measure what can be called **convergent thinking,** in the sense that there is just one correct answer to each question. Thus, definitions of words, questions of fact, arithmetic problems, puzzles, and block designs all require correct answers that are easily scored. Another type of intelligence test, in which the number and variety of responses to a single question rather than a single correct answer are emphasized, can measure **divergent thinking.** An example is a question asking for a list of the possible uses of a coat hanger. Frontal-lobe injury interferes with the intelligence required by divergent thinking, rather than the convergent type measured by standard IQ tests. Several lines of evidence support Guilford's idea.

Behavioral Spontaneity

Patients with frontal-lobe lesions have long been recognized to exhibit a loss of spontaneous speech. Various investigators have been able to quantify this loss by using tests such as the Thurstone Word-Fluency Test (also referred to as the Chicago Word-Fluency Test). Patients are asked to write or to say, first, as many words starting with a given letter as they can think of in 5 minutes and, then, as many four-letter words starting with a given letter in 4 minutes.

Patients with frontal-lobe lesions have a low output of words in this test. For example, when asked to generate as many words as he could think of beginning with a specific letter, E. L., introduced at the beginning of this chapter, sat for about 2 minutes before asking if he could use the Latin names of plants. He was assured that he could do so but, after another couple of minutes, he remarked, "I can't think of any!" He abandoned the plant names but, even with an additional 5 minutes, he could think of only six words.

Although the principal locus of this defect appears to be in the left orbital frontal region, lesions in the right orbital frontal region also may produce a marked reduction in verbal fluency. Again we see less asymmetry in the frontal lobes than we might expect. The following case is an example of low spontaneous verbal fluency resulting from a lesion of the right frontal lobe.


(A) Mrs. P's lists
(B) Normal control's lists

Note low output, shaky script, and rule breaking in the four-letter "c" words.

Figure 16.6 Word fluency. Subjects were given 5 minutes to write as many English words as possible starting with the letter "s" and 4 minutes to write as many four-letter words as possible starting with the letter "c."

Mrs. P., a 63-year-old woman with a college degree, was suffering from a large astrocytoma of the right frontal lobe. Her word fluency is reproduced in Figure 16.6A. Four features of frontal-lobe damage are illustrated in her test performance:

1. Her total output of words is remarkably low: only 8 words beginning with the letter "s" and 6 words beginning with the letter "c." (Control subjects of

similar age and education produce a total of about 60 words in the same time period, as shown in Figure 16.6B.)

2. Rule breaking is a common characteristic of patients on this test. We told Mrs. P. several times that the words starting with "c" could have only four letters. She replied. "Yes, yes, I know, I keep using more each time." Even though she understood the instructions, she could not organize her behavior to follow them successfully.
3. Her writing was not fluid but rather jerky, much like that seen in a child learning to write, implying that her tumor had invaded the motor or premotor cortex.
4. Mrs. P. insisted on talking throughout the test—complaining that she simply could not think of any more words—and kept looking around the room for objects starting with the required letter.

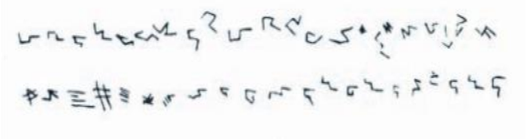
A study by Jones-Gotman and Milner raises the question of whether this verbal-fluency deficit might have a nonverbal analogue. The researchers devised an ingenious experiment in which they asked patients to draw as many different designs as they could in 5 minutes. The drawings were not supposed to be representational of anything, but rather much like the doodles that students are prone to put in the margins of their notes or textbooks. The patients were then asked to draw as many different designs as they could, but this time using only four lines (a circle was counted as a single line).

The results show a beautiful analogue to the verbal-fluency results. As can be seen in Figure 16.7, lesions in the right frontal lobe produced a large decrease in the number of different drawings produced. Normal controls drew about 35 drawings, left-frontal-lobe patients drew about 24 drawings, and right-frontal-lobe patients drew about 15 drawings. This deficit appears to be related to an impoverished output, high perseveration, and, in some cases, the drawing of nameable things (that is, representational drawings). As with verbal fluency, lesions in the orbital cortex or central facial area in the frontal lobe appeared to produce a larger deficit than did the more-dorsal lesions.

Figure 16.7 Design fluency. In an analog to the word-fluency test, subjects were allowed 5 minutes to draw as many nonrepresentational doodles as they could.

(A) Normal subject

(B) Frontal lobe patient showing perseveration



(C) Frontal lobe patient showing lack of spontaneity

It seems likely that frontal-lobe patients show reduced spontaneity not only in speech or doodling but in their behaviors in general. For example, Kolb and Taylor recorded the spontaneous behavior of frontal-lobe patients taking a battery of neuropsychological tests. Patients with frontal-lobe removals displayed fewer spontaneous facial movements and expressions than did normal controls or patients with more-posterior lesions. In addition, there were dramatic differences in the number of words spoken by the patients in a neuropsychological interview: patients with left frontal removals rarely spoke, whereas patients with right frontal lesions were excessively talkative.

Although the range of behaviors studied to date is small, there is reason to believe that frontal-lobe patients have a general loss of spontaneous behavior. Frontal-lobe patients characteristically appear lethargic or lazy: they often have difficulty getting out of bed in the morning, getting dressed, or initiating other daily activities such as going to work. One patient is a particularly dramatic example. He was a prominent lawyer who suffered a midline meningioma in the frontal lobe. The tumor was removed surgically, but he was left with bilateral damage to the superior aspect of both frontal lobes.

His IQ score was still superior (higher than 140), and his memory for legal matters was unimpaired. Nonetheless he was unable to function in his profession, because he could not get up in the morning to go to work, preferring to stay in bed and watch television. When his wife forced him to get up and go to work, he was disruptive at the office because he could not concentrate on any law-related work. Rather, he was distracted by anything else going on in the office. Curiously, he remained an excellent resource for his colleagues, who nonetheless found his behavior intolerable and consequently preferred to consult him by telephone.

Strategy Formation

Patients with frontal-lobe lesions are especially impaired at developing novel cognitive plans or strategies for solving problems. For example, when Shallice and Evans asked subjects questions that required reasoning based on general knowledge for which no immediate obvious strategy was available, they found that frontal-lobe patients did very poorly and often gave bizarre responses. In a later study, Shallice and Burgess gave patients a task very much like our dinner-party problem. The subjects were given a list of six errands (for example, "Buy a loaf of brown bread") and an instruction to be at a particular place 15 minutes after starting. They were also to get answers to four questions (for instance, the price of a pound of tomatoes). They were not to enter shops except to buy something and were to complete the tasks as quickly as possible, without rushing.

The frontal-lobe patients found this simple task very difficult. They were inefficient, they broke rules (for example, entered unnecessary shops), and two of the three patients failed at least four of the tasks. Yet, when quizzed, all the patients understood the task and attempted to comply. Similar difficulty with everyday problems is seen in a study by Smith and Milner. They asked subjects to estimate the average price of a particular object, such as a sewing machine. They suggested that to perform such a task one must develop a strategy that might include deciding what a typical sewing machine is, judging the range of possible prices, and selecting a representative price for a machine of average quality. They found that patients with frontal-lobe lesions—especially right frontal lesions—were very poor at this task. In contrast, patients with temporal-lobe damage who showed memory deficits on other tasks performed like controls on this task. Thus, it seems unlikely that a simple explanation of impaired memory will account for the poor performance of the frontal-lobe patients.

Shallice and Burgess argued that, although the frontal lobe may have a general role in planning behavior, it has a critical role in coping with novel situations in contrast with routine ones. They suggested that coping with a novel situation, by which they mean a novel set of external and internal states, entails the activation of a wide variety of processes to solve the problem. In contrast, the solution of a familiar task can rely on strategies that have been well practiced and therefore are more easily accessed.

The extreme case of novel situations is during development, when most situations are novel. Hebb noted in the 1940s that, relative to frontal-lobe injuries acquired in adulthood, people whose frontal-lobe injuries were acquired in childhood often show surprisingly severe deficits in behavioral control. He believed that these people were not able to properly develop the behavioral schematas necessary to solve problems. That is, they would find few situations routine.

Environmental Control of Behavior: Impaired Response Inhibition and Inflexible Behavior

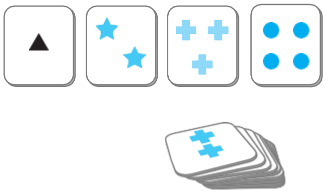
Perhaps the most commonly observed trait of frontal-lobe patients is their difficulty in using information from environmental cues (feedback) to regulate or change their behavior. This difficulty manifests itself in a number of ways.

Response Inhibition

Patients with frontal-lobe lesions consistently perseverate on responses in a variety of test situations, particularly those in which there are changing demands. The best example of this phenomenon is observed in the Wisconsin Card-Sorting Test, which has become one of the standard clinical tests of frontal-lobe injury. As Figure 16.8 shows, a subject is presented with four stimulus cards, bearing designs that differ in color, form, and number of elements. The subject's task is to sort the cards into piles in front of one or another of the stimulus cards. The only help given the subject is to be told whether the choice is correct or incorrect.

The test works on the following principle: the correct solution is, first, color; when the subject has figured out this solution, the correct solution then becomes, without warning, form. Thus, the subject must now inhibit classifying the cards on the basis of color and shift to form. When the subject has succeeded at selecting by form, the correct solution again changes unexpectedly, this time to the number of elements. It will later become color again, and so on.

Figure 16.8 The Wisconsin Card-Sorting Test, showing test material as presented to the subject. The task is to place each card from the bottom pile with the appropriate card in the top row, sorting by one of three possible categories: color, number of elements, or shape. Subjects are never told the correct sorting category but only whether their responses are correct or incorrect. When the subject selects the correct category, the correct solution changes unexpectedly. (After Milner, 1964.)



Shifting response strategies is particularly difficult for people with frontal lesions. They may continue responding to the original stimulus (color) for as many as 100 cards until testing is terminated. Throughout this period, they may comment that they know that color is no longer correct. They nevertheless continue to sort on the basis of color. For example, one person stated (correctly): "Form is probably the correct solution now so this [sorting to color] will be wrong, and this will be wrong, and wrong again."

Such perseveration is common on any task in which a frontal-lobe patient is required to shift response strategies, demonstrating that the frontal lobe is necessary for flexibility in behavior. It is important to note that, on card-sorting tasks, the subjects must not be given any hint that they are to expect a change in the correct solution, because many frontal-lobe patients improve dramatically when given this warning. The cue apparently allows enough flexibility in behavior to solve the problem.

From the results of Milner's work, the principal locus of this card-sorting effect appears to be roughly around Brodmann's area 9 in the left hemisphere. Lesions elsewhere in the left frontal lobe, and often in the right, will also produce a deficit on this task, although an attenuated one.

Performance of the Stroop Test (Figure 16.9) further demonstrates loss of response inhibition subsequent to frontal-lobe damage. Subjects are presented with a list of color words (blue, green, red, and so forth), each word being printed in colored ink but never in the color denoted by the word (for example, the word "yellow" is printed in blue, green, or red ink). The subject's task is to name the color in which each word is printed as quickly as possible. Correct response requires the inhibition of reading the color name, an inhibition that is difficult for many control subjects. Perret found that patients with left frontal lesions were unable to inhibit reading the words and thus were impaired in this task.

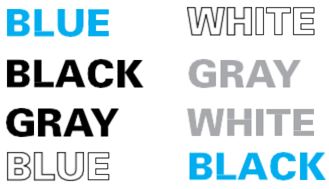


Figure 16.9 The Stroop test. The task is to give the color of the ink for each word as quickly as possible. When the ink color and the color name are the same, the task is simple. When they are different, there is a tendency to read the word rather than give the ink color.

Risk Taking and Rule Breaking

Frontal-lobe patients are distinguished from other patients in their common failure to comply with task instructions. Milner found this failure to comply to be especially common on tests of stylus-maze learning in which a buzzer indicates that the patient has made an error and is to stop and start at the beginning of the maze again. Subjects with frontal-lobe lesions tended to disregard the signal, thereby continuing the incorrect path and making more errors. This behavior is reminiscent of their inability to modify their responses in the card-sorting task.

Miller gave subjects a task in which words had to be guessed on the basis of partial information. With each additional clue, a subject was assigned a successively lower point value for a correct answer, but points could be collected only if the answer was correct. An incorrect answer forfeited all the points for an item. Frontal-lobe patients took more risks (and made more mistakes) than did other patients, and the risk taking was greatest in those frontal-lobe patients who also had temporal-lobe damage.

The role of the orbital frontal cortex in risk taking has been studied extensively by Antoine Bechera, Antonio Damasio and their colleagues, who designed a gambling task in which subjects gradually learn how to play a unique card game. They are presented with four decks of cards and are asked to turn over the first card in any deck. Some cards are associated with a payoff ($50 or $100), whereas other cards result in a $50 or $100 penalty being assessed. Each subject is given $2000 in play money to play the game, and the goal is to make as much money in the game as possible.

The trick in the game is that the reward and penalty contingencies of each deck differ. For example, one deck may have high payoffs but also has high penalties, whereas another may have a lower payoff but also a low penalty. The game is set so that playing two of the four decks results in a net loss, whereas playing the other two yields a net gain.

The results from the Bechera studies are clear: normal subjects and patients without frontal damage sample from all the decks for a while but quickly learn which decks have the best payoff. In contrast, patients with orbital frontal injuries do not learn this strategy and play predominantly from the bad decks, thus losing all their money. An important aspect of the task is that subjects are not allowed to keep a running tally of how they are doing; rather they must "sense" which decks are risky and which are profitable. This ability is clearly a function of the prefrontal cortex and its loss makes it difficult for orbital frontal patients to make wise decisions, especially in social or personal matters — that is, situations in which an exact calculation of future outcomes is not possible.

Self-regulation

We noted earlier that people with ventral frontal injuries, such as M. L., have deficits in the self-regulation of behavior in unstructured situations, in part because of a loss of autonoetic awareness. M. L. had been a salesman, and he knew what his job had been and that he had traveled a great deal. When pressed, however, he was unable to provide a single personal example of this job. For example, when asked if he traveled to conferences, he said that, yes, he traveled to conferences often; it was a major part of his job. Yet he could not name a single instance of an experience at a conference. His autobiographical knowledge was lost.

You can imagine what this impairment would be like if you think about your high-school experience. We are all aware of having gone to high school and can describe what high school was like, and presumably so could patients such as M. L. The difference, however, is that we can describe personal events that happened in high school, whereas M. L. would not be able to do so. We can immediately see why M. L. had difficulty in relating to his wife—he simply could not recall instances that would explain why they were married.

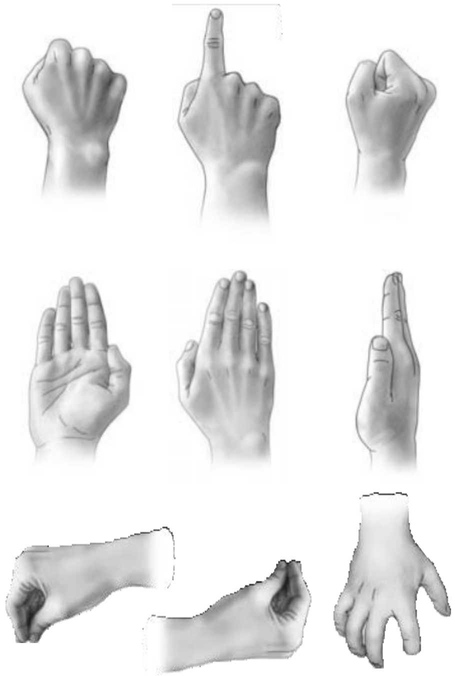


Figure 16.10 The nine hand postures that constitute responses in the Petrides experiments. In these studies, subjects had to learn to associate each hand posture with one of nine different colors and to perform the movement in response to the presentation of the appropriate color.

Associative Learning

Patients with large frontal-lobe lesions have often been claimed to be unable to regulate their behavior in response to external stimuli—that is, to learn from experience. Luria and Homskaya described patients with massive frontal-lobe tumors who could not be trained to respond consistently with the right hand to a red light and with the left hand to a green light, even though the patients could indicate which hand was which and could repeat the instructions.

In an extensive series of studies, Petrides examined the ability of both human patients and monkeys with frontal lesions to make arbitrary stimulus-response associations. In one study, Petrides asked frontal-lobe patients to learn arbitrary associations between colors and hand postures, as illustrated in Figure 16.10. For example, patients were presented with nine colored stimuli, and the their task was to learn which posture was associated with which colored stimulus. Damage to either the left or the right hemisphere resulted in poor performance on this task. Again, the behavioral impairments in the frontal-lobe patients could not be attributed to a deficit in memory, because temporal-lobe patients who performed poorly on other tests of memory performed normally at these tasks. Rather, the problem is in learning to select, from a set of competing responses, the appropriate ones for the various stimuli.

Poor Temporal Memory

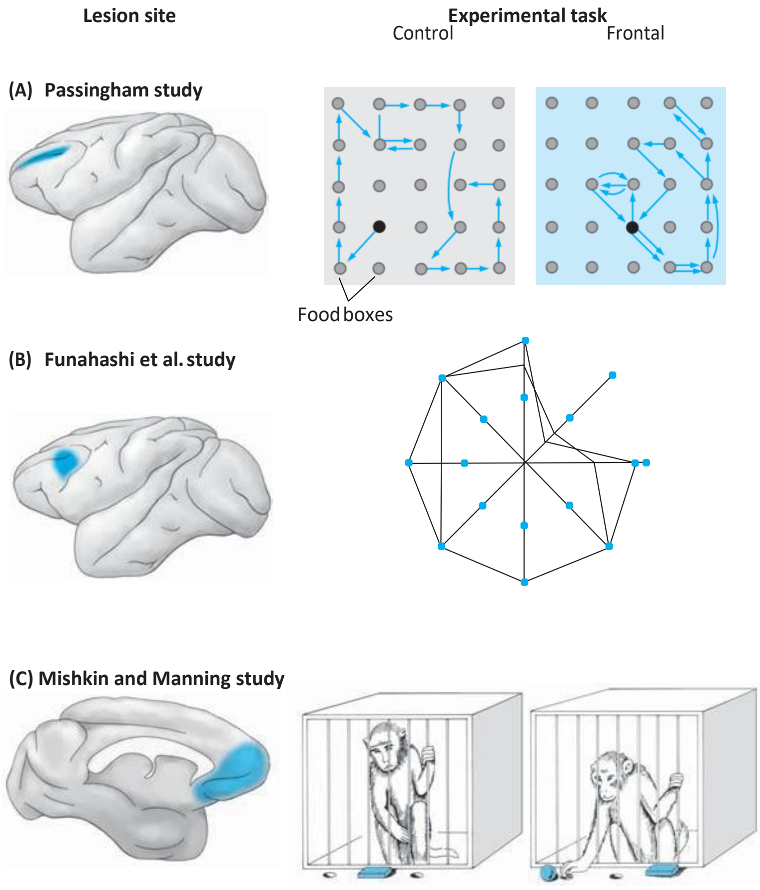
Perhaps the single most important experimental discovery for understanding the functions of the frontal lobe was Carlyle Jacobsen's finding that chimpanzees with frontal-lobe lesions were impaired in the delayed-response test. In this task, an animal observes a reward being placed under a plaque, in a well. The chimp's view is blocked for a few seconds, and then it is allowed to retrieve the reward. Animals with prefrontal lesions perform at chance, even with extended practice. Although the behavioral impairment is unlikely to be due to a single deficit, the deficit is difficult to interpret without recourse to some sort of memory difficulty. Four additional experiments are especially germane here.

In the first experiment, Passingham presented monkeys with a task in which the animals were required to open each of 25 doors to obtain a food reward. Food was placed behind each door only once per day; so the animals had to learn not to return to locations where the reward had been obtained already. Passingham found that lesions in area 46 produced marked impairments in this task. Thus, whereas the normal monkeys developed a door-opening strategy that led to few repetitions, the lesioned animals were inefficient, often returning to previously accessed doors (Figure 16.11A).

In the second experiment, Funahashi, Bruce, and Goldman-Rakic trained monkeys to fixate on a central spot of light while target lights were flashed in different parts of the visual field. The monkeys had to wait for the fixation spot to disappear before moving their eyes to the spot where the target light had been flashed. The researchers found that unilateral lesions in the principal sulcus (part of area 46) impaired the monkeys' ability to remember the location of the target in a restricted region of the contralateral visual field, as illustrated in Figure 6.11B. They interpret this result as showing that the principal sulcus contains a mechanism for guiding responses on the basis of stored information, which in this case is spatial.

The third experiment was conducted by Mishkin and Manning. They trained monkeys in a task known as delayed nonmatching to sample. In this test, a monkey is confronted with an unfamiliar object, which it displaces to

Figure 16.11 Testing for temporal memory. Schematic illustrations of frontal lesions in monkeys are shown at the left. The shaded areas represent lesion sites in three experiments, illustrated on the right, that reveal a temporal memory deficit. (A) Passingham study. (B) Funahashi et al. study. (C) Mishkin and Manning study.



1

The task is to retrieve a food reward from each of 25 food boxes. Notice that the control animal seldom returns to a previously visited location, whereas the monkey with a sulcus principalis lesion makes numerous errors.

2

The task is to fixate at the central point, and then after a 3 sec delay move the eye to locate the place where a target light had flashed. Correct performance percentage is indicated by the relative positions of the lines along axes drawn through the central fixation point. Note that the monkey performed poorly in one region of the visual field contralateral to the lesion.

3

The monkey is shown an object, which is displaced, and a food reward is obtained. The monkey is then presented with two objects after a short delay; the task is to obtain a reward, which is under the novel object. Monkeys with medial lesions are impaired at this task, which is nonspatial.

find a reward. After a delay the animal sees the same object paired with a new one. The monkey must recognize the object that it saw earlier and move the new one instead to get a reward (Figure 6.11C). Monkeys with lesions of areas 10 and 32 are impaired in this task. Mishkin and Manning interpret this result as showing that this area of the frontal cortex participates in the short-term storage of object information.

The fourth experiment was a 1991 study by Petrides in which monkeys were given two different tasks. In the first task, the animals were presented with three objects and allowed to choose one for reward. The animals were then given an option between the chosen object and one of the other objects, with the correct choice being the one that was not previously selected. In the second task, the animals were again presented with three objects and allowed one choice. On this task, however, they were then presented with the previously selected object and a novel object.

In the first task, a monkey must recall what it did with the objects. In the second task, the monkey must recall only which object was seen before. Monkeys with dorsolateral lesions performed at chance on the first task but performed as well as controls on the second. This result suggests that the dorsolateral cortex plays a role in monitoring self-generated responses.

Taken together, these five experiments point to an unequivocal role for the frontal cortex in short-term memory process and to the fact that different regions of the prefrontal cortex control the storage of different types of information. In view of the anatomical connections, it seems likely that area 46 plays a role in providing an internal representation of spatial information and that the medial regions play a similar role with object information.

The results of electrophysiological studies lend further support for the role of area 46: cells in this area are active during the intervals in delayed-response tests and their activity ends abruptly when the animal responds. Some neurons respond selectively to the spatial position of the cues, and we might expect to find similar neurons coding some features of objects as well.

Studies of temporal memory have taken a slightly different slant with human subjects. On the basis of earlier works by others, Milner, Corsi, and Leonard designed an ingenious test of memory for the order in which things have happened, which is often called recency memory. Subjects were shown a long series of cards, each card bearing two stimulus items, which were either words or pictures. On some cards a question mark appeared between the items, and the subjects' task was to indicate which of the two items had been seen more recently. Successful performance required the subjects to recall the order of presentation of the stimuli.

On most test trials, both the items had appeared previously, but, on some, one item was new. In this case, the task became one of simple recognition memory. Patients with frontal-lobe lesions performed normally on the recognition trials, but they were impaired in judging the relative recency of two previously seen items. Further, there is relative asymmetry in the frontal lobes in this regard: the right frontal lobe appears to be more important for memory for nonverbal or pictorial recency; the left frontal lobe appears to be more important for verbal recency. In contrast, patients with temporal-lobe lesions were impaired in the recognition test but not in the recency test. (This latter finding is curious, because it seems to be analogous to blindsight in that people who fail to recognize items can identify which was observed most recently.

Might this suggest a memory location system that is separate from a memory recognition system?)

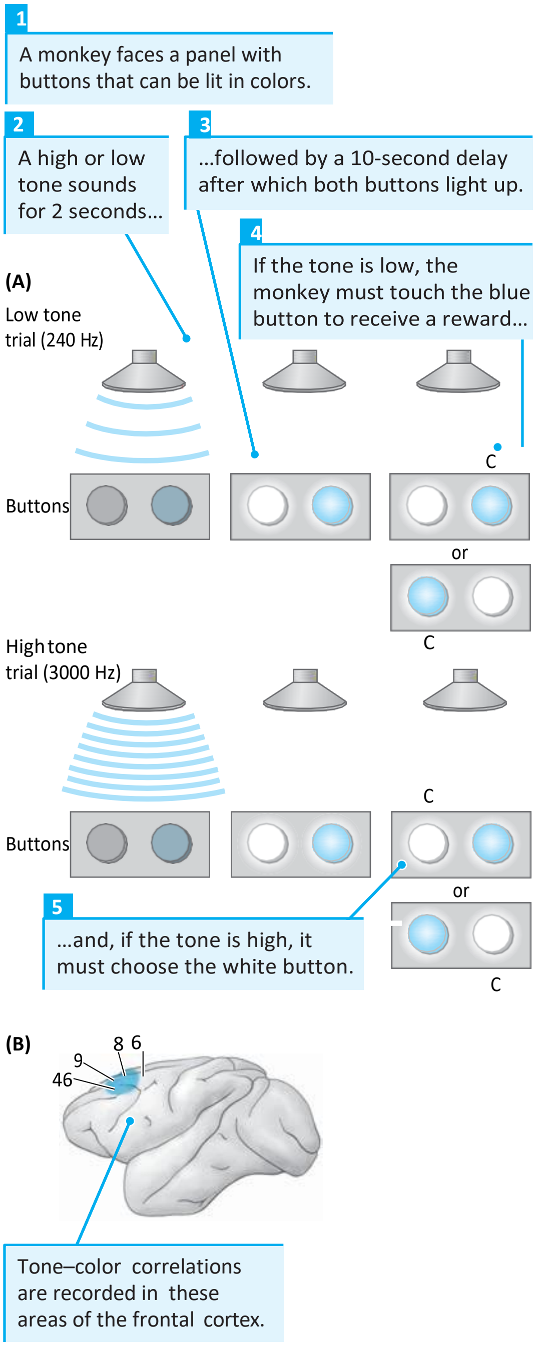
Petrides and Milner designed an experiment that is conceptually similar to Passingham's self-ordering task for monkeys. Subjects were presented with stacks of cards on which were displayed an array of 12 stimuli, including words or drawings in parallel versions of the task. The stimuli in the array remained constant, but the position of each stimulus varied randomly from card to card. The subjects' task appeared rather simple: go through the stack and point to only one item on each card, taking care not to point to the same item twice. Thus, the subjects themselves initiated the plan to follow and determined the order of responding. Although the task appears easy to us, frontal-lobe patients did not find it so: left-frontal-lobe lesions were associated with impaired performance of both verbal and nonverbal versions of the task, whereas right-frontal-lobe lesions were associated with poor performance only on the nonverbal test.

Petrides and Milner suggested that, in contrast with the recency tests, the self-ordered tasks require subjects to organize and carry out a sequence of responses. From the moment the subjects begin to respond, they must constantly compare the responses that they have made with those that still remain to be carried out. Hence, the self-ordered task demands an accurate memory as well as an organized strategy.

When questioned about their approach to the task at the end of testing, patients with frontal lesions were less likely than other subjects to report that they had used a particular strategy, and, when they had, the strategy often appeared to be ill defined and to have been used inconsistently. The deficit is unlikely to have been one of simple memory, because temporal-lobe patients, who would have been expected to have defects of memory, performed normally at this task.

The temporal memory deficits in both laboratory animals and in human patients have caught the imagination of researchers for more than 60 years. Recently, both imaging studies and single-unit studies in monkeys have confirmed what the lesion studies had suggested — namely, that the prefrontal cortex plays a critical role in temporal memory. A study by Fuster and colleagues serves as a nice illustration. In this experiment, monkeys were trained to associate two different tones each with one of two different colors, as illustrated in Figure 16.12. The trick was that a monkey heard the tone and then had to remember which tone it had heard for 10 seconds before making a response to obtain reward. A large contingent of cells in dorsolateral prefrontal area (areas 8, 9, and 46) responded selectively to one tone or the other and, later, to its associated color. These cells appear to integrate sound and color across time. Curiously, in trials on which the animals made errors, the cells failed to respond, indicating no temporal correlation of the sound and color.

Figure 16.12 Prefrontal cells that code sensory associations.



1 A monkey faces a panel with buttons that can be lit in colors.

2 A high or low tone sounds for 2 seconds...

3 ...followed by a 10-second delay after which both buttons light up.

4 If the tone is low, the monkey must touch the blue button to receive a reward...

5 ...and, if the tone is high, it must choose the white button.

Tone–color correlations are recorded in these areas of the frontal cortex.

Impaired Social and Sexual Behavior

Social and sexual behaviors require flexible responses that are highly dependent on contextual cues. It is hardly surprising, therefore, that frontal-lobe lesions interfere with both. Perhaps the most obvious and striking effect of frontal-lobe damage in humans is a marked change in social behavior and personality. The most publicized example of personality change subsequent to frontal-lobe lesions is that of Phineas Gage, first reported by John Harlow in 1868. Gage was a dynamite worker who survived an explosion that blasted an iron tamping bar (about a meter long and 3 centimeters wide at its widest point) through the front of his head (Figure 16.13). After the accident, his behavior changed completely. Gage had been of average intelligence and was "energetic and persistent in executing all of his plans of operation." His personality after the injury was described by Harlow as follows:

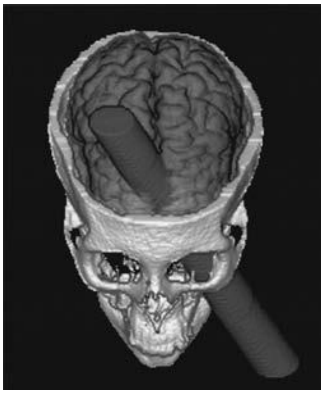


Figure 16.13 When Phineas Gage died in 1861, no autopsy was performed, but his skull was later recovered. Measurements from Gage's skull were combined with imaging techniques to reconstruct the accident and determine the probable location of the lesioning. The image makes it obvious that the frontal cortex of both hemispheres was damaged. (Department of Neurology and Image Analysis Facility, University of Iowa.)

> The equilibrium or balance, so to speak, between his intellectual faculties and animal propensities seems to have been destroyed. He is fitful, irreverent, indulging at times in the grossest profanity, manifesting but little deference to his fellows, impatient of restraint or advice when it conflicts with his desires, at times pertinaciously obstinate, yet capricious and vacillating, devising many plans of operation, which are no sooner arranged than they are abandoned in turn for others appearing more feasible. A child in his intellectual capacity and manifestations, he has the animal passions of a strong man. (Blumer and Benson, 1975, p. 153)

Gage's injury affected primarily the left frontal lobe from the medial orbital region upward to the precentral region. Although Gage's skull has been examined carefully, the first person with extensive frontal damage to undergo close scrutiny at autopsy was a furrier who fell 30 meters from a window. He suffered a compound fracture of the frontal bones and severe injury to the right frontal lobe but, remarkably, was never unconscious and was confused only briefly. Before the fall, the man had been good natured and sociable, but, afterward, he became nasty and cantankerous. Autopsy, about a year after the accident, revealed deep scarring of the orbital part of both frontal lobes, although it was more extensive on the right.

From 1900 until about 1950, there were many excellent psychiatric studies of the effect of brain lesions on personality. A consistent finding of this work (especially Kleist's, cited in Zangwill) was that damage to the orbital regions of the frontal lobe is associated with more-dramatic changes in personality than are dorsolateral lesions, although the latter also have significant effects. Clinical descriptions of the effects of frontal-lobe lesions on personality abound, but there are few systematic studies.

At least two types of personality change have been clinically observed in such patients: Blumer and Benson have termed them **pseudodepression** and **pseudopsychopathy.** Patients classified as being pseudodepressed exhibit such symptoms as outward apathy and indifference, loss of initiative, reduced sexual interest, little overt emotion, and little or no verbal output. Patients classified as pseudopsychopathic exhibit immature behavior, lack of tact and restraint, coarse language, promiscuous sexual behavior, increased motor activity, and a general lack of social graces. Two case histories illustrate these personalities.

Pseudodepression

> At the age of 46, a successful salesman sustained a compound depressed fracture of the left frontal bone in a traffic accident. Treatment included debridement [surgical removal] and amputation of the left frontal pole. Recovery was slow, and 9 months after the injury he was referred for long-term custodial management. By this time, he had recovered motor function with only a minimal limp and slight hyperreflexia on the right side, had normal sensation, no evidence of aphasia, and normal memory and cognitive ability (IQ 118). Nonetheless, he remained under hospital care because of marked changes in personal habits.
>
> Prior to the accident, the patient had been garrulous, enjoyed people, had many friends and talked freely. He was active in community affairs, including Little League, church activities, men's clubs, and so forth. It was stated by one acquaintance that the patient had a true charisma, "whenever he entered a room there was a change in the atmosphere, everything became more animated, happy and friendly."
>
> Following the head injury, he was quiet and remote. He would speak when spoken to and made sensible replies but would then lapse into silence. He made no friends on the ward, spent most of his time sitting alone smoking. He was frequently incontinent of urine, occasionally of stool. He remained unconcerned about either and was frequently found soaking wet, calmly sitting and smoking. If asked, he would matter-of-factly state that he had not been able to get to the bathroom in time but that this didn't bother him. Because of objectionable eating habits he always ate alone on the ward. His sleep pattern was reversed; he stayed up much of the night and slept during the day. He did not resent being awakened or questioned. He could discuss many subjects intelligently, but was never known to initiate either a conversation or a request. He could give detailed accounts of his life prior to the accident, of the hospitals he had been in, the doctors and treatment he had had, but there was an unreality to his conversation. When asked, he would deny illness, state emphatically that he could return to work at any time, and that the only reason he was not working was that he was being held in the hospital by the doctors. At no time did he request a discharge or weekend pass. He was totally unconcerned about his wife and children. Formerly a warm and loving father, he did not seem to care about his family. Eventually, the family ceased visiting because of his indifference and unconcern. (Blumer and Benson, 1975, pp. 156–157)

Pseudopsychopathy

> A 32-year-old white male was admitted for behavioral evaluation. History revealed that he had sustained a gunshot wound in Vietnam 5 years previously. A high-velocity missile had entered the left temple and emerged through the right orbit. Infection necessitated surgical removal of most of the orbital surface of the right frontal lobe. On recovery, he was neither paralyzed nor aphasic but suffered a remarkable change in personality.
>
> Prior to injury he had been quiet, intelligent, proper, and compulsive. He was a West Point graduate and spent the ensuing years as a military officer attaining the rank of captain. Both as a cadet and later

> as an officer, he was known to be quiet, strict, and rigid. He was considered a good commander, trusted by his men, but never shared camaraderie with his troops or with his peers.
>
> Subsequent to injury, he was outspoken, facetious, brash, and disrespectful. There was no evidence of self-pity, although he frequently made rather morbid jokes about his condition (for example, "dummy's head"). On admission to the hospital, he had just failed at an extremely simple job.
>
> He was not aphasic but misused words in a manner that suggested inability to maintain specific meanings. For instance, when asked whether the injury had affected his thinking his response was, "Yeah—it's affected the way I think—it's affected my senses—the only things I can taste are sugar and salt—I can't detect a pungent odor—ha ha—to tell you the truth it's a blessing this way." When the examiner persisted, "How had it affected the way you think?" his response was "Yes—I'm not as spry on my feet as I was before." He was never incontinent, but did show a messiness in attire. His remarks to the nurses and other female personnel were open and frank but were never blatantly sexual. His premorbid IQ was reported at about 130. Present examination showed a full-scale IQ of 113. (Blumer and Benson, 1974, pp. 155–156)

Blumer and Benson are probably correct in their assertion that all elements of these syndromes are observable only after bilateral frontal-lobe damage. Nevertheless, some elements of these two rather different syndromes can be observed in most, if not all, persons with unilateral frontal-lobe lesions. Pseudodepression appears most likely to follow lesions of the left frontal lobe, pseudopsychopathic behavior to follow lesions of the right frontal lobe.

Changes in sexual behavior are among the most difficult symptoms of frontal-lobe damage to document properly, largely because of social taboos against investigating people's sexual lives. To date, there are no such empirical studies, but there is anecdotal evidence that frontal lesions do alter libido and related behavior. Orbital frontal lesions may introduce abnormal sexual behavior (such as public masturbation) by reducing inhibitions, although the frequency of sexual behavior is not affected. On the other hand, dorsolateral lesions appear to reduce interest in sexual behavior, although patients are still capable of the necessary motor acts and can perform sexually if led through the activity "step by step."

The results of several studies show that frontal-lobe lesions in monkeys significantly alter social behavior. In one interesting study, Butter and Snyder removed the dominant (so-called alpha) male from each of several groups of monkeys. They removed the frontal lobes from half of these alpha monkeys. When the animals were later returned to their groups, they all resumed the position of dominant male, but within a couple of days all the monkeys without frontal lobes were deposed and fell to the bottom of the group hierarchy.

Analogous studies of wild monkeys have shown similar results: monkeys with frontal-lobe lesions fall to the bottom of the group hierarchy and eventually die, because they are helpless alone. Exactly how the social behavior of these animals changed is not known, but there is little doubt that the changes are as dramatic as those in the social behavior of humans. The social interactions of monkeys are complex and include a significant amount of context-dependent behavior; the behavior of a monkey will change in accord with the configuration of the proximal social group, and monkeys may lose this ability after frontal-lobe lesions. There are likely to be additional components of this behavioral change, however, that relate to the interpretation of species-typical sensory cues, whether they be odors, facial expressions, or sounds.

The deficit in the perception of facial expression by frontal-lobe patients may be related to the loss of cells that code for facial expression. Certain cells in the temporal lobe are especially responsive to facial expression (see Chapter 15), and Rolls and his colleagues showed that a population of cells in the orbital frontal cortex also codes for faces. Some of these face-selective neurons are responsive to facial expression or movement. It is thus not surprising that patients with orbital frontal lesions might have difficulty in understanding facial expression. We could speculate that there are also likely to be cells in the prefrontal cortex that are responsive to tone of voice, which would be a verbal analogue of facial expression.

Is There a Spatial Deficit?

We have indicated that a key to understanding the functions of the dorsolateral cortex is to be found in its relation to the posterior parietal cortex. The posterior parietal cortex plays a central role in visuomotor guidance of movements in space, and region PG and the superior temporal sulcus play some role in more-complex spatial behavior such as mental rotation (see Chapter 14). These parietotemporal regions provide a major input into the dorsolateral region, which implies some role of this frontal area in spatially guided behavior.

The precise role has been difficult to determine, however. It is clear that dorsolateral lesions impair short-term memory for the location of events, and this deficit presumably could interfere with the selection of behaviors with respect to places in space. Indeed, the delayed-response deficit, as well as the deficit in Passingham's and Goldman-Rakic's tasks (see Figure 16.11), have spatial components.

The role of the dorsolateral cortex in "spatial thinking" can also be seen in a blood-flow study by Roland and Frieberg. They asked subjects to imagine walking along a familiar route and taking first a left turn, then a right, and so on, alternating turns along the path. A major increase in blood flow in the dorsolateral region suggests a role for the dorsolateral cortex in the selection of spatially guided behaviors.

Taken together, results of the blood-flow and lesion studies suggest that the frontal lobe has a role in selecting between different visual locations. This role may be related to some aspect of attention, an idea that we return to in Chapter 22. Note, however, that little evidence favors the role of the prefrontal cortex in parietal-lobe functions such as topographic orientation or in the ability to mentally manipulate or organize spatial information (see Chapter 14).

Symptoms Associated with Damage to the Facial Area

Through the years, Taylor and his colleagues have accumulated some remarkable data from a small group of patients with localized surgical removals of the precentral and postcentral gyri, containing, respectively, the motor and sensory representations of the face (see Figure 16.1D). Unlike the removal of cortical areas for the hand, the removal of areas for the face is seldom associated with long-lasting somatosensory deficits on the face, even if both the sensory and the motor representations are removed completely. This finding is in keeping with the evidence that the face is represented bilaterally in the cortex.

There has been no systematic study of the facial motor abilities of patients who have undergone the removal of both precentral and postcentral gyri, but Kolb and Milner found such patients able to perform facial-movement sequences normally. Furthermore, although these patients had difficulty in making individual facial movements in the initial postoperative period, especially on the side of the face contralateral to the lesion, they appeared to have regained normal voluntary facial control a month after surgery, although closer examination might have revealed subtle defects. In addition, their faces were expressive, and they displayed normal spontaneous facial expressions at frequencies well within normal limits.

In the immediate postoperative period, patients with left-hemisphere facial-area lesions are aphasic, being impaired at both language comprehension and language production, as well as being alexic. However, these symptoms subside rapidly, probably having resulted from swelling and trauma associated with the surgical procedure. Within about 6 months to a year after surgery, only a slight residual expressive dysphasia remains. Yet these same patients are severely impaired at certain other language tests. In particular, they perform very poorly on tests of word fluency and are unable to make effective use of the phonetic elements of language.

In addition, these same patients are very poor spellers, occasionally writing words that are unrecognizable. Their low verbal fluency is complemented by a very low design fluency (see Figure 16.7). Patients with right facial-area lesions are worse at design fluency than are patients with very large anterior frontal lesions. This lack of spontaneity in verbal and design fluency is remarkable, considering the normal spontaneity of facial expressions.

In summary, unilateral removal of the cortical area representing the face results in no significant chronic loss in sensory or motor control of the face, presumably because of the face's bilateral representation in the cortex. But it does result surprisingly in chronic deficits in phonetic discrimination, spelling, verbal fluency, and design fluency. Taylor has preliminary data suggesting that these deficits may result primarily from damage to the precentral motor representation of the face, rather than from damage to the postcentral sensory representation. The origin of these deficits, however, is unexplained to date.

Clinical Neuropsychological Assessment of Frontal-Lobe Damage

Considering the number and variety of symptoms associated with frontal-lobe damage, surprisingly few standardized neuropsychological tests are useful for assessing frontal-lobe function. Furthermore, some of the symptoms of frontal-lobe injury, such as the loss of self- regulation of behavior, are not easily assessed by a neuropsychological test. Nonetheless, there are a number of very good clinical tests, which are summarized in Table 16.3. As with the parietal- and temporal-lobe tests discussed in Chapters 14 and 15, for a person to perform normally on all these tests if there were damage to either frontal lobe would be highly unusual.

The Wisconsin Card-Sorting Test (see Figure 16.8) is the best available test of dorsolateral frontal cortex function. As described earlier, a subject is told to sort the cards into piles in front of one or another of the stimulus cards bearing designs that differ in color, form, and number of elements. The correct so-

Table 16.3 Standardized clinical neuropsychological tests for frontal-lobe damage

Function	Test	Basic reference
Response inhibition	Wisconsin Card Sorting	Milner, 1964
	Stroop	Perret, 1974
Verbal fluency	Thurstone Word Fluency	Milner, 1964 Ramier and Hecaen, 1970
Nonverbal fluency	Design Fluency	Jones-Gotman and Milner, 1977
Motor	Hand dynamometry	Taylor, 1979
	Finger tapping	Reitan and Davison, 1974
	Sequencing	Kolb and Milner, 1981
Language comprehension	Token	de Renzi and Faglioni, 1978
	Spelling	Taylor, 1979
	Phonetic discrimination	Taylor, 1979
Working memory	Self-ordering	Owen et al., 1990 Pouchon et al., 2001
Planning	Tower of London	Owen et al., 1995

lution shifts without the subject's knowledge when he or she has figured out each solution.

Recall that the Thurstone Word-Fluency Test requires subjects to say or write as many words beginning with a given letter as possible in 5 minutes, and then as many four-letter words beginning with a given letter in 4 minutes (see Figure 16.6). Although subjects with lesions anywhere in the prefrontal cortex are apt to do poorly on this test, subjects with facial-area lesions perform the worst, and those with orbital lesions perform only slightly better. Performance is poorest when the lesion is in the left hemisphere.

The Gotman-Milner Design-Fluency Test (see Figure 16.7) also is very useful, although somewhat difficult to score. Subjects are asked to draw as many unnameable, abstract drawings as they can in 5 minutes. Frontal-lobe patients will draw very few items, draw nameable objects, or draw the same figure repeatedly. Like the verbal-fluency tests, the design-fluency task appears most sensitive to orbital injury.

Two tests, the Tower of Hanoi and the Tower of London, have proved sensitive to frontal injury, although the Tower of London appears to be a purer test of planning functions. In both tests, a person is presented with several pegs and several discs of varying size. The discs must be moved from the presented location to another configuration and location according to different rules. For example, only one disc can be moved at a time, and a large disc may never be placed on a smaller one. Damage to either the left or the right prefrontal cortex produces impairments on these tasks.

Tests of motor function include tests of strength (hand dynamometry), finger-tapping speed, and movement sequencing. Strength and finger-tapping speed are significantly reduced contralaterally to a lesion that is in the vicinity of the precentral or postcentral gyri. Motor sequencing can be assessed by using Kolb and Milner's facial-sequence test, although this test requires considerable practice to administer and scoring should be from videotaped records. Simpler tests of movement programming such as the Kimura Box Test (see Chapter 14) are not suitable, because frontal-lobe patients are unlikely to perform very poorly unless the lesion extends into the basal ganglia.

As in preceding chapters, we recommend the token test as a quick screening test for aphasia, to be followed if necessary by more-extensive aphasia testing (see Chapter 19). Although damage to Broca's area is widely believed to result in deficits only in language production and not in comprehension, this outcome is not strictly true. Left frontal lesions in the vicinity of Broca's area produce deficits in comprehension as well as in production.

Spelling is seriously impaired by facial-area lesions and can be assessed by any standardized spelling test. Phonetic differentiation, a test described by Stitt and Huntington and used for neurological patients by Taylor, is another means of assessing facial-area function. A series of nonsense words, such as "agma," is presented and a subject's task is to identify the first consonant sound. This test proves difficult even for controls, but it is performed most poorly by subjects with facial-area damage, especially damage on the left side. However, frontal-lobe lesions outside the facial area also may impair performance on this test significantly.

In the absence of language deficits, localizing frontal-lobe damage in either the left or the right hemisphere with neuropsychological tests may prove to be difficult, presumably because the functions of the two frontal lobes overlap significantly. Clinical evaluation of personality as pseudodepressed or pseudopsychopathic (as discussed earlier) may prove useful in localizing the dysfunction to the left or the right hemisphere, respectively, but caution is advised. Unfortunately, no standardized quantitative measures of these symptoms are available.

Imaging Frontal-Lobe Function

In general, the results of imaging studies have shown specific activation for prefrontal functions that were identified historically in lesion studies, as illustrated in Table 16.4. Thus, for example, the results of many studies have shown dorsolateral prefrontal participation in tasks tapping verbal and nonverbal working temporal memory. An especially intriguing finding, however, comes

Table 16.4 Examples of functional imaging studies of frontal-lobe function

Presumed function	Locus of activation	Basic reference
Self-ordering	Dorsolateral	Petrides, 2000
Conditioned learning	Dorsolateral	
Spatial working memory	Dorsolateral; Ventrolateral	Owen et al., 1996
Visuomotor skill learning	Dorsolateral	Doyon et al., 1996
Verbal memory retrieval	Dorsolateral	Buckner et al., 1995 Tulving et al., 1994
	Ventrolateral	Petrides et al., 1995
Encoding visual information	Orbital frontal	Frey and Petrides, 2000
Encoding unpleasant auditory information	Orbital frontal	Frey et al., 2000
Facial expression or recognition or both	Inferior prefrontal	Idaka et al., 2001

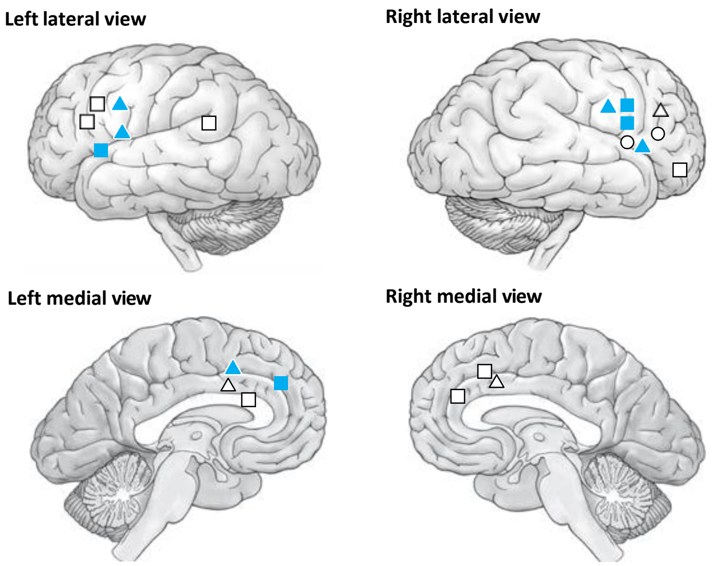


Figure 16.14 Prefrontal activations produced by widely different cognitive demands. Shown are lateral and medial views of each hemisphere. Despite the diversity of cognitive demands in these experiments, frontal activations show apparent clustering, with most points within middorsolateral, midventrolateral, and dorsal anterior cingulate regions.

from a review by Duncan and Owen. They reviewed the patterns of frontal-lobe activation associated with a broad range of different cognitive demands, including aspects of perception, response selection, executive functions, working memory, long-term memory, and problem solving.

Given such a diverse set of presumed cognitive functions, one can reasonably imagine that different regions of the frontal lobe are active during the performance of cognitive tasks that require different cognitive functions. The surprising finding, however, is that a striking regularity in activation emerged: for most cognitive demands, there was a similar recruitment of the dorsolateral, ventrolateral, and anterior cingulate regions, as summarized in Figure 16.14. The reviewers concluded that, although regional specialization exists within the frontal lobe, a frontal lobe network is consistently recruited for the solution of a diverse set of cognitive problems. How these three regions work in concert to produce behavior is not immediately obvious, but the overlap of activation in such diverse cognitive processes makes it easy to see how the frontal lobe is central to the control of such a diversity of behavior.

Diseases Affecting the Frontal Lobe

Many symptoms of frontal-lobe injury are characteristic of people with psychiatric or neurological disorders, including especially schizophrenia (see Chapter 20), Parkinson's disease (see Chapter 22), and Korsakoff's disease (see Chapter 18). In each case, a disturbance of frontal-lobe function likely contributes significantly to the behavioral symptoms of the disease.

In schizophrenia, there are believed to be an abnormality in the mesocortical dopamine projection, which terminates largely in the frontal lobe, a decrease in blood flow to the frontal lobe, and possible frontal-lobe atrophy. Schizophrenic patients perform poorly on all tests of frontal-lobe function and exhibit abnormalities in the control of eye movements, but they perform normally on tests of parietal-lobe function.

Parkinson's disease results from a loss of the dopamine cells of the substan- tia nigra. Although the primary projection of these cells is to the caudate nu- cleus, they project directly to the prefrontal cortex, too, and indirectly through the dorsomedial nucleus of the thalamus. Parkinson patients are characterized by a lack of facial expression similar to that seen in frontal-lobe patients, and they are impaired in the Wisconsin Card-Sorting Test and at delayed-response tasks.

Korsakoff patients suffer from alcohol-induced damage to the dorsomedial thalamus and may have a deficiency in catecholamines in the frontal cortex. They perform poorly on the Wisconsin Card-Sorting Test, as well as on tests of spatial memory such as delayed response.

Summary

The frontal lobe can be conceived as the end point for the visuomotor and object-recognition functions that are initiated in the occipital lobe. The frontal lobe's function in these processes is to select behaviors with respect to context and internalized knowledge.

It is possible to subdivide the frontal lobe into three distinct functional zones: motor cortex, premotor cortex, and prefrontal cortex. The motor cor- tex is responsible for making movements. The premotor cortex selects movements. The prefrontal cortex controls the cognitive processes so that appropriate movements are selected at the correct time and place. The pre- motor cortex can be divided into two regions: the lateral area responsible for selecting behaviors in response to environmental cues and the supplementary area responsible for selecting behaviors on the basis of internalized knowledge. The prefrontal cortex can be divided into two general zones: a dorsolateral zone responsible for selecting behavior with respect to temporal memory and the inferior prefrontal region responsible for selecting behavior with respect to context. Context may be current or based on previous knowledge, including self-knowledge.

The wide range of symptoms of frontal-lobe lesions can be grouped, conceptually, into several categories: (1) disturbances of motor functions;

(1) loss of divergent thinking; (3) impaired response inhibition and inflexible behavior; (4) poor temporal memory; and (5) impaired social and sexual be- havior imaging.

There is a complementary effect of left and right frontal lesions, in that left frontal lesions are more likely to affect language or movement-related behav- iors, and right frontal lesions are more likely to alter nonlanguage functions, such as emotion.

The results of imaging studies show frontal participation in tasks with widely different cognitive demands including attentional tasks, sensory discrimination tasks, motor tasks, spatial problem solving; and semantic processing of words. Dysfunction of the frontal lobe is implicated in many behavioral disorders, including particularly schizophrenia, Parkinson’s disease, and Korsakoff’s disease.